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Vegetation, soil, and groundwater characteristics of wetlands in the Nebraska Sandhills

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by

Nanette Eileen Rayapati Erickson

A Thesis Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of

MASTER OF SCIENCE

Department: Botany
Major: Botany (Aquatic and Wetland Ecology)

Signatures have been redacted for privacy

Iowa State University
Ames, Iowa

1992

For Sasha

This above all: to thine own self be true,
And it must follow, as the night the day,
Thou canst not then be false to any man.

William Shakespeare (Hamlet, I,iii,78-80)

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PREFACE

The Song of the Pine Creek Settlers[1]

I've reached the land of drouth and heat,
Where nothing grows for man to eat,
The wind that blows with burning heat,
O'er all our land is hard to beat

O! Nebraska land, sweet Nebraska land!
As on your burning soil I stand,
I look away across the plains,
And wonder why it never rains,
Till Gabriel calls, with trumpet sound,
And says the rain has gone around.

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[1] Sandoz, M. 1935. Old Jules. Hastings House, New York York, USA; 1985 reprint, Bison Books, University of Nebraska Press, Lincoln, Nebraska, USA. Page 152.

GENERAL INTRODUCTION

The Nebraska Sandhills are the largest sand-dune complex in the western hemisphere. This region is a mosaic of mixed-grass prairie and wetlands, with approximately 557,590 ha of wetlands (Keech and Bentall 1978). Most of these wetlands are groundwater-fed, and have been impacted by groundwater depletion. Although over 30% of Sandhill wetland habitats was lost by 1986, the region remains a critical area for waterfowl nesting and migration, as well as habitat for other wildlife. The ability to delineate these wetlands thus is imperative for their protection and management.

The National Ecology Research Center of the U.S. Fish and Wildlife Service supported an ecological study of wetlands in the Nebraska Sandhills from 1988 to 1991. The purpose of this study was to document relationships among vegetation, soil, and groundwater hydrology. The study was performed at and around Crescent Lake National Wildlife Refuge in the western Sandhills. In 1988, a general vegetation survey was conducted at 16 lakes. In 1989, vegetation and other parameters were sampled at regular intervals from 19 groundwater well sites around Roundup and Island lakes within the refuge. Additional experimental work was performed in 1989 and 1990. The relationship of vegetation data to soil and groundwater parameters was described using two approaches.

Vegetation and Soils

Correspondence between vegetation and soil data is an assumption throughout a series of procedures commonly known as the "unified federal method" (Federal Interagency Committee for Wetland Delineation 1989). However, Sandhill wetlands may be difficult to delineate because many are composed of Entisol soils that lack typical hydric characteristics. Because of recent losses of Sandhill wetland habitats, accurate delineation is more critical than ever. This study tested the hypothesis that soil and vegetation data in the Nebraska Sandhills are comparable, and therefore the unified federal method can be used to accurately designate boundaries of these wetlands.

The "comprehensive onsite determination method" portion of the unified federal method for wetland delineation was the source for subsequent vegetation and soil analyses. Field data were collected in 1988 and 1989. Vegetation quadrats (0.5 m^2) were sampled along transects at 13 lakes in 1988. Vegetation composition and environmental parameters were monitored weekly in 1989 from permanent quadrats at two lakes within the refuge. Plant species within quadrats were identified and percent cover was estimated for each species; soils then were identified by Soil Conservation Service personnel.

Vegetation composition of each quadrat was described by a prevalence index, which weighted species by their percent cover and relative frequencies of occurrence in wetlands. Prevalence indices subsequently were calculated for each soil series; General Linear Models procedures for analysis of variance and Duncan's multiple range tests indicated whether vegetation data and soil identity were comparable. Finally, hydrology data were compared to soil and vegetation data to determine how useful certain hydrologic parameters would be when delineating Sandhill wetlands.

Vegetation and Groundwater

Vegetation distributions appear to correspond to known groundwater gradients that occur both locally and regionally in the western Sandhills. On a regional scale, specific conductance of groundwater decreases along an elevational gradient; thus, lakes at higher elevations have higher levels of specific conductance than do lower lakes. Locally, gradients develop within individual lakes between north and south shores as a result of evapotranspiration. This study tested the hypothesis that plant distributions observed in wetlands of the Nebraska Sandhills corresponded to differences in groundwater chemistry associated with these gradients. The relationship between vegetation patterns and groundwater was ascertained through a series of field investigations and laboratory experiments.

Plant composition was examined in 1988 from 16 lakes along an elevational gradient in order to identify recurrent distribution patterns. In 1989, vegetation data was collected from 19 well sites at two lakes. These sites also were monitored for depth to water table, specific conductance, pH, and soil moisture content. Cumulative covers were calculated by species for north and south shores of lakes to determine whether species distribution in 1988 and 1989 were random. Correlation analysis then was used to indicate relationships among dominant plant species and the environmental parameters measured in 1989.

A number of experiments (i.e., reciprocal transplanting, seed germination, seedling growth, and seed bank recruitment) examined whether various life-history stages of selected wetland plant species were affected by water chemistry treatments having different concentrations of dissolved salts. A chi-square goodness-of-fit test indicated whether high and low salt concentrations characteristic of south and north lake shores, respectively, affected survival of transplants of four species (i.e., Scirpus americanus, Scirpus fluviatilis, Distichlis spicata, and Spartina pectinata). Seeds of Carex scoparia, Carex scoparia, Carex praegracilis, Scirpus americanus, Scirpus maritimus, and Distichlis spicata were germinated in 10 water chemistry treatments over a wide range of salt concentrations. Analysis of variance procedures for balanced designs indicated whether water treatments affected germination. Seedlings of *Carex scoparia* and *Scirpus maritimus* likewise were grown in 10 water chemistry treatments; analyses were similar to that for the germination study. Soil samples containing the seed bank were subjected to two water chemistry treatments consisting of high and low salt concentrations. Effects of water treatments on the number of *Scirpus acutus* and *Typha* spp. recruitment was determined through analysis of variance procedures for balanced designs.

Explanation of Thesis Format

An alternate thesis format has been used. The thesis consists of two manuscripts that examine the relationships among vegetation, soil, and groundwater in the Sandhills of Nebraska. Preceding the manuscripts is the "General Introduction" that describes the purpose of the study and an overview of data analysis used within each manuscript. Following the manuscripts is a "General Summary" that is a synopsis of the results and interpretation of data analysis for each manuscript. Literature cited within the General Introduction follows the General Summary section.

The manuscript styles follow that of the journal Ecology. The first manuscript addresses whether the unified federal method for delineating wetlands is applicable to Sandhill wetlands, and is titled "Utility of the 'unified federal method' for delineating wetlands in the Nebraska Sandhills." The second examines the relationship between groundwater chemistry gradients and wetland vegetation in the Sandhills; it is titled "Vegetation composition and groundwater in the Sandhills of Nebraska." Both manuscripts have joint authorship. Nanette E. R. Erickson, the first author and candidate for the degree of Master of Science, was responsible for designing the study, collecting, analyzing, and interpreting all data, and writing the manuscripts. Dr. Arnold G. van der Valk, the second author and major professor, assisted in designing the study and its analysis, and was the primary editor of the manuscripts.

PART I

UTILITY OF THE "UNIFIED FEDERAL METHOD" FOR DELINEATING WETLANDS IN THE NEBRASKA SANDHILLS

UTILITY OF THE "UNIFIED FEDERAL METHOD" FOR DELINEATING WETLANDS IN THE NEBRASKA SANDHILLS

Nanette E. R. Erickson and Arnold G. van der Valk, Department of Botany, 353 Bessey Hall, Iowa State University, Ames, Iowa 50011 USA

ABSTRACT. We examined the use of the unified federal method for delineating wetland boundaries at, and adjacent to the Crescent Lake National Wildlife Refuge in the western Nebraska Sandhills. Vegetation along a wetland-to-upland transition was sampled using quadrats around 13 lakes in 1988. Vegetation composition and environmental parameters were monitored weekly in 1989 in permanent quadrats at two lakes within the refuge.

Prevalence indices based on species abundance and frequencies of occurrence were calculated for quadrats located in areas within a particular soil series. Generally, there was a good correspondence between soils and vegetation composition. Prevalence indices calculated weekly in 1989 changed very little during the growing season. This suggests that one-time onsite inspections should be adequate for establishing wetland boundaries for the Sandhills. Two upland soils supported predominantly wetland vegetation. One upland soil, the Dailey series, occurred on a disturbed site;

however, the unmodified unified federal method is not suitable for disturbed sites. The second, the Els series, possibly has been misclassified as an upland soil, as it displays colors and mottling within the definition of a hydric soil.

We also examined how direct and indirect measures of wetland hydrology compared to Sandhill vegetation and soil. Both vegetation and soils data were related to the direct (i.e., depth to water table) and indirect (i.e., soil moisture content) measures of hydrology. However, vegetation and hydrology were related more closely than soil and hydrology. Furthermore, hydric and upland soil series could be distinguished by depth to water table but not by soil moisture content. For example, mean soil moisture contents for the hydric Tryon series were not significantly different from the upland Els series. Finally, in the unified federal method, a wetland must have less than 45.7 cm (18.0 in) to water table. For Sandhill wetlands, though, depths less than 75.0 cm (29.5 in) would be more realistic.

key words: wetland delineation, vegetation, hydric soils, Nebraska Sandhills

INTRODUCTION

The Sandhills of Nebraska are the largest continuous sand-dune complex in the western hemisphere, covering about 52,000 km^2 of the northern part of the State (Keech and Bentall 1978) (Figure 1). Vegetation of the Sandhills is comprised of a mosaic of mixed-grass prairie and wetlands, with approximately 557,590 ha of wetlands (Rundquist et al. 1981). Most wetlands are groundwater-fed (Ginsberg 1984); these wetlands have been impacted by groundwater depletion brought about by center pivot irrigation and its associated ditching, leveling, and filling. Groundwater depletion is considered the primary cause of wetland habitat destruction in the Sandhills. By 1986, wetland losses were estimated in excess of 30% for the entire Sandhills region, with losses over 90% in Loup County in the eastern Sandhills (Gersib, personal communication).

In spite of these losses, wetlands in the Nebraska Sandhills still provide critical nesting and migration sites for millions of waterfowl, songbirds, and shorebirds (Wolfe 1984), as well as habitats for fish and terrestrial wildlife (Rundquist 1983, Novacek 1989). The Sandhills were listed as one of 34 geographic areas of concern in the North American Waterfowl Management Plan adopted by the United States and Canada in 1985. They are considered by the Nebraska Game and Parks Commission to be the most important waterfowl production area in the state (Gersib, personal communication). The ability to delineate wetlands of the Sandhills is critical to their protection and management.

A federal task force consisting of representatives from the U.S. Army Corps of Engineers, U.S. Environmental Protection Agency, U.S. Fish and Wildlife Service, and U.S. Department of Agriculture, Soil Conservation Service constructed a guideline for wetland habitat delineation (Federal Interagency Committee for Wetland Delineation 1989). This guideline, hereafter referred to as the "unified federal method" (Wetland Training Institute, Inc. 1989) uses three criteria to designate a wetland: hydrophytic vegetation, hydric soil, and wetland hydrology (Federal Interagency Committee for Wetland Delineation 1989:5). Hydrophytic vegetation is defined as "macrophytic plant life growing in water, soil, or on a substrate that is at least periodically deficient in oxygen as a result of excessive water content." Hydric soils are those that are "saturated, flooded, or ponded long enough during the growing season to develop anaerobic conditions." Wetland hydrology involves "permanent or periodic inundation or soil saturation to the surface...." Of the three criteria, hydrology is most difficult to document due to annual, seasonal, or daily fluctuations.

According to the unified federal method, a one-time assessment of vegetation and soils is adequate for wetland delineation. A predecessor to the unified federal method initially was tested in the Nebraska Sandhills by Erickson and Leslie (1986). Their study indicated that selected hydric soils did support wetland vegetation; thus, vegetation and soil data could be used to delineate wetland boundaries in the Sandhills. However, the 1989 version of the unified federal method identified Entisols (i.e., relatively young soils without a developed B horizon) as a problems area for wetland delineation (Federal Interagency Committee for Wetland Delineation 1989:58). Hydric soils within this order are difficult to recognize in the field because they lack typical hydric characteristics. Unfortunately, because Entisols comprise a large portion of the Sandhills, the potential is great for wrongly delineating Sandhill wetland boundaries.

Although Erickson and Leslie (1986) collected data from selected lakes across the entire Sandhills, they did not document potential changes in vegetation composition over the growing season. For example, only six lakes were sampled over a four-day period at Crescent Lake National Wildlife Refuge in the western Sandhills. Furthermore, since the inception of the unified federal method, the Environmental Protection Agency (unpublished draft) has voiced several concerns, particularly in regard to the wetland hydrology criterion. By definition, the wetland hydrology criterion is met when the area is saturated to the surface or inundated for usually one week or more during the growing season (Federal Interagency Committee for Wetland Delineation 1989:7). One concern is that seven days of saturation or inundation are not enough to create a wetland. Another concern is that sites with dry soil surfaces are considered wetlands if the water table is within 45.7 cm (18.0 in) of the surface. We have attempted to address these concerns.

We tested the hypothesis that data for vegetation and soils, particularly Entisols, are comparable, and hence that the unified federal method is applicable to wetlands of the Nebraska Sandhills. We also examined whether seasonal variations in vegetation composition affected our results. We further examined whether duration-of-saturation and depth-to-water-table criteria (as defined in the 1989 version of the unified federal method) were valid for these wetlands. Finally, we tested whether an indirect estimate of hydrology satisfied the wetland hydrology criterion, and how indirect and direct measures of wetland hydrology compared at our study area.

We sampled the vegetation gradient at 13 lakes from prairie to emergent wetland, and their associated soils. We also sampled flora for seven weeks in permanent quadrats adjacent to 19 groundwater wells at two lakes to examine seasonal changes in vegetation composition. We also measured depth to water table, pH, specific conductance, and soil moisture content associated with the groundwater wells.

STUDY AREA

30 miles to water,
20 miles to wood,
10 miles to hell,
And I gone there for good[1]

Vegetation of the Sandhills

The Nebraska Sandhills have a semiarid climate. Evapotranspiration and precipitation patterns indicate a surplus of moisture from late fall to early spring, but a moisture deficit during the remainder of the year (Wilhite and Hubbard 1990). Mean annual precipitation ranges from 63.5 cm in the east to 37.6 cm in the west (Rundquist 1983). Mean annual temperature ranges from 9.4^{o} C in the east to 8.9^{o} C in the west (Wilhite and Hubbard 1990). Annual temperatures range from -40.0^{o} C in January to 43.3^{o} C in July (Rundquist 1983). Approximately 80% of the precipitation falls between April and September; however, nearly 75% of all annual precipitation is lost via evaporation or transpiration (Rundquist 1983). In part, the climate has restricted land use primarily to rangeland, although row cropping is possible with center-pivot irrigation.

The Nebraska Sandhills is one of the most extensive tracts of the North American grassland biome extant (Barnes

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[1] A verse carved on the door of a deserted shack near Chadron, Nebraska in the 1890s (Sandoz 1935:213)

and Harrison 1982). Most native vegetation is in either prairie or wetland, but scattered pockets of pine and deciduous forest also occur throughout the Sandhills. According to Kaul (1990:128), when viewed "as individual species, most of the flora of the Sand Hills is not particularly unusual, but the particular association of plants found in the Sand Hills makes this flora unique." An estimated 720 vascular plant species occur in the Sandhills, of which 670 species are native and 50 are introduced (Kaul 1990:127). Hayden's or blow-out penstemon (Penstemon haydenii) is the only species endemic to the Sandhills and the state of Nebraska. A number of boreal plant species found in the Sandhills are assumed to be relicts that survived from Pleistocene boreal forests (Kaul 1990). Overall, the number of species is relatively low when compared to other grassland habitats, but relatively high if compared to other areas with similar sandy, infertile soils (Kaul 1990).

At the turn of the 20th century, there was a debate as to whether the Sandhills originally were forested or not. Bessey (1896, as cited in Pool 1914) was a proponent of the forest theory, and recommended reforesting the region to restore what he perceived to be the natural vegetation. Rydberg (1895:145-146) supported Bessey's claim, citing pine logs buried in the sand as proof of prior forestation; he likewise advocated forest restoration. Attempts by Bessey to forest the

Sandhills were met with skepticism and opposition from ranchers, who resented use of the grasslands for anything other than cattle grazing, as well as by many scientists and politicians (Keech and Bentall 1978). Nevertheless, Bessey obtained and planted a 30,000 ac (12,141 ha) forest reserve in 1902, where he had some success in growing timber species (Keech and Bentall 1978). Many other individuals obtained "tree claims" from the government, but most failed to grow trees. Rydberg (1895) suggested that these individuals failed because they cultivated their plots as they would prairie soils, which destroyed the fragile soils and created blow-outs. Some 80 years later, Wells and Stewart (1987, as cited in Bleed 1990) provided fossil evidence that central and western Nebraska indeed were covered by an open pine parkland in the late Pleistocene epoch until around 18,000 years before present. However, climate at the time most likely was cooler and wetter than at present (Bleed 1990); thus, it is unlikely that large-scale reforestation would be successful today.

The Sandhills were explored botanically only prior to the turn of the 20th century. Webber (1889), under the direction of Charles Bessey, initially documented the vegetation of the central Sandhills region. The first thorough documentation of western Sandhills flora was performed by Rydberg (1895). He categorized the vegetation as "sand-hill," "dry-valley," "wet-valley," or "aquatic flora."

The first ecological study of the area was conducted by Pool (1914), who divided Sandhill vegetation into "upland formations" and "lowland formations." The upland formations included "prairie-grass," "short-grass," "woodland," "broadleaf forest," and "yellow pine," whereas the "water-plant," "marsh," and "meadow" formations constituted the lowlands. He also distinguished between alkaline and freshwater ponds and lakes, and attributed the lack of floating and submergent plants in some lakes in Cherry County to high alkalinity. Pool (1914:291) described the appearance of the meadow formation as a "highly developed . . . belt or a series of belts about lakes and ponds and in the lower valleys in many parts of the Sandhills." Pool (1914:293) also suggested that soil moisture and alkalinity gradients affected species distribution in the meadow formation. A decrease in soil moisture and receding water table apparently were associated with changes in vegetation composition of the marsh formation (Pool 1914:307).

For several years, vegetation studies of Sandhill wetlands focused primarily on species distribution (Tolstead 1942, Kolstad 1966). However, loss of wetland habitat in the Sandhills has sparked interest in wetland protection and the subsequent need for accurate delineation. Remote sensing was used by Rundquist (1983) to quantify historical changes in Sandhill wetland acreage. Gilbert et al. (1980) used remote sensing to delineate selected Sandhill wetlands in Cherry County, but obtained only marginal results. Problems with resolution and incompatible classification resulted in an over-estimation of their subirrigated meadow class and under-estimation of open water and marsh habitats. Gilbert et al. (1980) attributed these results to using photographic and satellite data taken during September rather than the onset of the growing season.

Field investigations of vegetation composition have proven more useful in delineating wetlands. Boundaries of wetlands in Garfield and Wheeler Counties were established using vegetation zones (i.e., xeric, mesic, or hydric) (U.S. Army Corps of Engineers 1983). Two studies in Nebraska specifically have used vegetation and soil data to separate wetland from upland sites. The Rainwater Basin in southern Nebraska has been the site of an ongoing cooperative delineation project conducted by the U.S. Army Corps of Engineers, Environmental Protection Agency, Nebraska Game and Parks Commission, and the U.S. Fish and Wildlife Service. Erickson and Leslie (1986) also studied vegetation and soil relationships in wetlands of both the Rainwater Basin and the Nebraska Sandhills, which provided the U.S. Fish and Wildlife Service with baseline data for evaluating wetland identification techniques.

Soils of the Sandhills

Four geological processes have shaped the Sandhill landscape: 1) marine processes; 2) alluvial processes; 3) aeolian processes; and 4) volcanic activity (Swinehart and Diffendal 1990). The Sandhills region was a marine environment during the Jurassic and Cretaceous periods (ca 65 million years ago), as evidenced by deposits of shales, chalks, and limestones. Changes during the Eocene-Paleocene epochs (ca 37-65 million years ago) of the Tertiary period are not documented by fossil or other geological records; however, soil formation is believed to have occurred during this time. From 37 million years to present, alluvial and aeolian forces shaped the Sandhills. Albeit, volcanoes have not had any influence on the Sandhills until recently, when Mount St. Helens deposited ash onto the area in 1980.

The present-day dune formations of the Sandhills are relatively young but composed of older materials. The parent material, alluvial sediments, were deposited during the Pliocene (ca 1.6-5.0 million years before present) by a precursor of the North Platte River, and they accumulated for at least one million years (Swinehart and Diffendal 1990). These sand and gravel deposits originated from regions near the Laramie Mountains in southeastern Wyoming, the Snowy Range in southcentral Wyoming, and northcentral Colorado. Dune formations are believed to have occurred no earlier than

10,000 years before present; dune orientation began an estimated 7,000 years ago as a result of prevailing northwest winds (Swinehart 1984). Dunes of the Sandhills are stabilized by prairie vegetation. Swinehart (1990:51) predicted that reducing vegetation to 20% cover would create large-scale dunes and an active "sand sea." Modern sand seas such as the Rub'al Khali of Saudi Arabia and the Takla Makan of China, however, receive less than 10 cm precipitation annually. Most soils of the Sandhills are highly erodible, and soil "blowouts" occur readily if vegetation cover is insufficient or disturbed. At the turn of the 20th century, Rydberg (1895) documented blowouts of 100 m diameter and 15 m to 20 m deep.

The soils encountered in our study were Mollisols, Entisols, and Inceptisols (Appendix A). Mollisols are prairie soils that have a prominent mollic epipedon. Aquolls, such as the Hoffland and Loup series, are Mollisols that are naturally wet, and have a dominantly low chroma matrix and high-contrast mottles below a black or dark greyish brown epipedon (Soil Conservation Service 1975). They commonly develop in low places where water collects and stands, but some are on seepy hillsides. Vegetation usually consists of grasses, sedges, and forbs. The Hoffland series is a Calciaquoll, typified by a shallow calcic or gypsic horizon (Soil Conservation Service 1975).

Ustolls are more or less freely drained Mollisols. Most rainfall comes during the growing season, but often it is erratic; drought is frequent and may be severe (Soil Conservation Service 1975). The Dailey series is a Haplustoll, which is formed in late-Pleistocene or Holocene deposits or on surfaces of comparable age. Vegetation of the Haplustolls is dominantly grasses and forbs.

The Entisols are undeveloped soils characterized by A and C horizons but no B horizon. Psamments are Entisols characterized by well sorted sands of shifting or stabilized sand dunes (Soil Conservation Service 1975). These soils typically are of recent to Pliocene age or older. Psamments have a low water-holding capacity; when dry and bare, they are subject to blowing and drifting. The Ustipsamments have an ustic moisture regime (i.e., moisture usually is present only during the growing season), and typically support grass or savanna vegetation (Soil Conservation Service 1975). Three soils (i.e., Ipage, Els, and Valentine) in our study were classified as Ustipsamments.

Aquents are wet Entisols found where the soil is continuously saturated with water. Both the Marlake and Tryon series are Aquents. The Marlake is classified further as a Fluvaquent. These soils are found primarily in floodplains and deltas and have sediments of Holocene age. The soils have a relatively high content of organic carbon at considerable depths in comparison to other wet mineral soils (Soil Conservation Service 1975). Psammaquents, such as the Tryon series, are Aquents with sandy texture that formed in late Pleistocene to recent sediments. The water table is at or near the surface of the soil for long periods unless artificially drained (Soil Conservation Service 1975).

The Wildhorse series is a Haplaquept. The Aquepts are wet Inceptisols with poor to very poor drainage. The Haplaquepts do not have a fragipan. However, the groundwater table usually is close to the surface at some time during the year, but not in all seasons (Soil Conservation Service 1975). These soils are composed of primarily late Pleistocene or Holocene sediments.

Lakes of the Sandhills

The Sandhills contain an estimated 2,500 lakes, both permanent and ephemeral; in dry years, this number may drop to 1,500 (Bleed and Ginsberg 1990)[2]. Lakes throughout the Sandhills are generally small, although they may reach lengths and widths of 4.8 km and 1.6 km, respectively (Bleed and Ginsberg 1990). Most lakes of the Sandhills are shallow, with mean depths of 0.8 to 1.2 m; Blue Lake within Crescent Lake

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[2] An extensive description of lakes is found in part II, "Vegetation composition and groundwater in the Sandhills of Nebraska;" portions have been repeated as reference

National Wildlife Refuge is the deepest known at 4.3 m (McCarraher 1977). Ginsberg (1984) characterized three types of lakes in the Sandhills: 1) groundwater lakes, 2) lakes with little connection to groundwater, and 3) perched lakes with no groundwater connection. Sandhill lakes range in alkalinity from almost zero to greater than 90,000 mg/l, one of the highest alkalinities measured in natural lakes (Schnagl 1980, as cited by Bleed and Ginsberg 1990).

Water chemistry gradients often correspond to groundwater movements through the Sandhills. Winter (1989) stated that groundwater moves through Sandhill lake chains in response to differences in elevation, with groundwater seepage from higher toward lower lakes. Chemical differences associated with this phenomenon have been documented; lakes at higher elevations have registered specific conductance readings of 10,000 μS/cm, compared to less than 1,000 μS/cm for lower lakes (Winter, personal communication, as cited by LaBaugh 1986). Chemical gradients associated with groundwater flow also occur within individual lake basins. Groundwater discharge occurs where the water table slopes into a lake, usually along the north shore, whereas recharge occurs as the water table slopes away from the lake, usually along the south shore. However, because evaporation exceeds precipitation in the Sandhills during much of the year, a conductivity gradient develops where the groundwater recharge contains a greater concentration of dissolved salts relative to discharge. Hence, water associated with the south shore has a higher specific conductance than that of water associated with the north shore.

Study Site

Our study site was located in Garden County, Nebraska, in the western Sandhills (Figure 1). Most samples were collected in and around Crescent Lake National Wildlife Refuge. This 18,630 ha refuge was established in 1938 primarily for the purpose of waterfowl management. In 1988, vegetation of 13 lakes was surveyed: Goose, Gimlet, Roundup, Hackberry, Island, Christ, Crane, and Blue lakes located within the refuge boundaries; Crescent Lake located south of the refuge; and Miller, Maverick, Wolf, and Hessey lakes to the north (Figure 2). In 1989, vegetation and environmental parameters were sampled weekly in association with 19 groundwater wells around Roundup and Island Lakes (Figure 3). Roundup Lake had two wells on the north shore and three wells on the south. Island Lake had two parallel well lines on the north shore, each with four wells, and two lines on the south shore, each with three wells.

METHODS

1988 Vegetation Data

Vegetation was surveyed between June and August 1988. Five transects were positioned at both the north and south shore of each lake. Transects began at the upland prairie and ended at the lake littoral zone. Five quadrats (0.5 m^2) were sampled along each transect: a quadrat was placed at each end of the transect, and three additional quadrats were placed at even intervals between the two ends. Plant species within quadrats were identified and percent cover was estimated for each species. The Great Plains Flora Association (1986) was used for plant nomenclature. Locations of 650 quadrats were marked with survey flags for later verification of soil mapping units. The soils were classified to series in August 1988 by a soil scientist from the Garden County Soil Survey Office, Soil Conservation Service.

1989 Vegetation Data

The primary emphasis of our 1989 study was to examine the relationship between plant species and environmental parameters measured at groundwater wells (see below, "Water chemistry and depth measurements" and "Soil moisture content"). We selected sites located within vegetation zones around Roundup and Island lakes in August 1988; at each site, soil pedons were classified to series by a Soil Conservation

Service soil scientist. Four permanent vegetation quadrats ($0.5\ m^2$) were spaced at 1-m intervals along a line parallel to the lake shore, with the well at the center of the line. Percent cover was estimated for each species; quadrats were examined weekly for species composition.

Use of the Unified Federal Method

The sampling scheme generally followed the specifications given for the quadrat sampling procedure of the "comprehensive onsite determination method" (Federal Interagency Committee for Wetland Delineation 1989:39). However, these data were collected in 1988, prior to the publication of the unified federal method. Deviations from the comprehensive method are as follows:

1) five transects were established on both north and south shores of each lake;

2) the number of sample quadrats per transect was held constant at five, regardless of the length of the transect;

3) all plant species within the quadrat were identified, rather than 50% of the total dominance as recommended in the guide; and

4) Daubenmire (1968) cover classes (i.e., 0 = < 1%, 1 = 1-5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, and 6 = 96-100%) were assigned rather than the cover classes

stipulated in the guide. This made it possible to compare our 1988 and 1989 data to that in Erickson and Leslie (1986).

Data were analyzed using SAS on the Iowa State University mainframe computer. The General Linear Models procedure for analysis of variance tested the effects of transect location (as determined by lake and shore position) and soil identity on vegetation composition. Duncan's multiple range tests showed whether hydric and upland soils supported wetland vegetation to different degrees, as stipulated in the unified federal method. Vegetation composition of each quadrat was described by a prevalence index. The equation used to calculate the index was:

$$PI = (F_o + 2F_{fw} + 3F_f + 4F_{fu} + 5F_u) / (F_o + F_{fw} + F_f + F_{fu} + F_u);$$

where: PI = prevalence index; F_o = frequency of occurrence of obligate plant species; F_{fw} = frequency of occurrence of facultative wetland species; F_f = frequency of occurrence of facultative species; F_{fu} = frequency of occurrence of facultative upland species; and F_u = frequency of occurrence of upland plant species (Federal Interagency Committee for Wetland Delineation 1989:48). Species were assigned indicator groups (e.g., obligate, facultative wetland) according to Reed (1988) (Table 1). Soils where the prevalence index is less than 3.00 are considered to support primarily hydrophytic vegetation, and these sites were designated as wetlands.

Soils with an index greater than 3.00 were designated as non-wetland.

Groundwater Well Installation

Eighteen groundwater wells were installed in August 1988 and June 1989 by the U.S. Geological Survey; one well already was in place. Well lines were established at the north (two wells) and south (three wells) shores of Roundup Lake. Two parallel lines were located at the north shore (four wells each), and two more lines were at the south shore (three wells each). We assigned a three to four letter code representing the lake and shore position (e.g., RO-S for Roundup Lake, south shore). A number indicated relative position in the well line; wells assigned smaller numbers occurred closer to the open water habitat, whereas wells with larger numbers were in upland habitat.

Individual wells were constructed from a 61.0-cm-long (2.0 ft) PVC screen (10-slot, 0.03 cm [0.01 in] mesh) glued with PVC cement onto a PVC pipe of 5.1-cm (2.0 in) diameter. Well length was based on the estimated depth to groundwater at a site. Holes were hand-augered to a depth approximately 1 m below the water table. Wells were inserted into their holes; bentonite fill was used to prevent downward water movement.

Defining Vegetation Zones

In August 1988, we visually defined the vegetation bands around Roundup and Island lakes at Crescent Lake National Wildlife Refuge. Soil cores taken within the bands were then identified by a Soil Conservation Service soil scientist. Nineteen sites within the vegetation bands were chosen as sites for groundwater wells. For statistical purposes, we grouped the well sites into one of three vegetation zones: "emergent," "wet meadow," or "upland." Vegetation zones were defined primarily using vegetation composition, but also soils, hydrology, and topography. We defined the emergent zone as having predominantly obligate wetland species (see Table 1) and inundated soils. The wet meadow was defined as transitional between the emergent and upland zones; sites in this zone had a mixture of wetland and upland vegetation, and saturated soils. Finally, we assigned wells to the upland zone that had primarily upland vegetation and occurred in unsaturated soils. In 1989, vegetation was sampled weekly from the four permanent quadrats adjacent to the wells, with percent cover estimates made for all species.

Water Chemistry and Depth Measurements

Wells were monitored on a weekly to bimonthly basis from June through August 1989. We measured depth to water table with a weighted 30.1 m (100.0 ft) metal tape, and recorded values to the nearest 2.5 cm (1.0 in); surface water depths were not incorporated into these measurements. Water samples from the wells were collected using a Nalgene hand-operated vacuum pump. Specific conductance was measured in the field with a Hanna HI 8333 conductivity meter; samples were stirred gently when measured. Water samples then were taken to the field laboratory and analyzed for pH using an Orion portable pH meter (model SA 250). A Ross pH electrode was used in conjunction with an automatic temperature compensation probe. Prior to sampling, the probe was calibrated manually using buffers of pH 7 and 10. Samples were stirred gently while pH was determined. Weekly measurements were discontinued on 15 August 1989.

Soil Moisture Content

Soil cores were collected weekly to bimonthly from June to August 1989. Cores measuring approximately 3.8 cm (1.5 in) diameter and 20.3 cm (8.0 in) length were taken with a soil probe. Soils were collected from the four permanent vegetation quadrats at each well site, placed into preweighed soil tins, and returned to the field laboratory. Cores were weighed wet, then placed in a drying oven (approximately 80^{o} C) for 8-10 hours. Samples were reweighed, and percent water content was calculated for each sample. Weekly measurements were discontinued on 15 August 1989.

Analyses of Vegetation and Environmental Parameters

The 1989 data were used to calculate means for the environmental parameters of individual wells and their soil series. Means for vegetation zones (i.e., emergent, wet meadow, and upland) also were calculated from individual well site means. We then applied General Linear Models procedures for analysis of variance to test effects of soil series identity on individual environmental parameters (i.e., depth to water table, specific conductance, pH, and soil moisture content), and effects of vegetation zones on these environmental parameters. Duncan's multiple range tests then indicated respective differences among soil series and zones for individual environmental parameters.

RESULTS

The Unified Federal Method

Nine soil series were encountered in our 1988 study (Table 2); of these, four are recognized by the Soil Conservation Service (1985) as hydric soils (i.e., Hoffland, Loup, Marlake, and Tryon)[4]. The remaining five soils were upland soils of the class Psamment, which are relatively young sandy soils with poorly formed A and no B horizons. In 1989, three of the five soil series present are recognized as hydric (i.e., Hoffland, Marlake, and Tryon). Detailed descriptions of all soil series are given in Appendix A.

In 1988, 159 plant species were found in 650 quadrats. Fifty-nine species were identified from 76 quadrats measured weekly from 19 wells in 1989. The number of species found in quadrats within each soil series is given in Table 3.

The General Linear Models procedure for analysis of variance for 1988 prevalence index data indicated that soil series ($F_{8,648} = 209.27$, prob > F = 0.0001) and transect location ($F_{12,648} = 5.17$, prob > F = 0.0001), as determined by lake and shore position, were both significant variables

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[4] The Federal Interagency Committee for Wetland Delineation (1989:18) cautions that although a soil is listed as hydric, this does not necessarily mean that the wetland hydrology criterion has been met, nor does exclusion of a soil from the list mean that the wetland hydrology criterion has not been met; however, inclusion on the list indicates that those soils typically meet the hydrology criterion

(Table 4). Duncan's multiple range tests indicated significant differences among mean prevalence indices for samples from hydric and upland soils (Table 5).

Analysis of the 1989 prevalence index data also indicated that soil series ($F_{4,531}$ = 322.76, prob > F = 0.0001) and transect location ($F_{3,531}$ = 36.16, prob > F = 0.0001) were significant variables (Table 6). Duncan's multiple range tests also indicated significant differences among mean prevalence indices for samples from hydric and upland soils (Table 7).

Weekly calculations of prevalence indices indicated significant differences among hydric and upland soil series throughout the growing season (prob > F = 0.0001) (Table 8). Some differences were observed in the Duncan groupings (e.g., soils of the Hoffland series were not significantly different from either Tryon or Marlake in week 1), but the soil order (based on prevalence index) remained constant (Table 8). Prevalence indices fluctuated within individual soil series; for example, for the Marlake series from 1.20 to 1.21 and in the Hoffland series from 1.57 to 2.04.

The prevalence indices calculated for 1986, 1988, and 1989 data consistently indicated that the hydric soils supported wetland vegetation (i.e., PI < 3.00), with the exception of soils in the Tryon series in 1986 (Table 9). However, not all upland soils scored above 3.00. Soils of the nonhydric Dailey soil series in 1988 had a mean of 2.91 (N = 12). In 1988, the upland Els soils had scores less than 3.00 at Blue (2.34, N = 6), Crane (2.98, N = 13), and Goose (2.91, N = 10) lakes (Appendix B). The Els series in 1989 had a mean prevalence index of 2.71, with a weekly range of 2.60 to 2.83 (Tables 7 and 8, respectively).

Vegetation and Environmental Parameters

We assigned six wells to the upland zone, seven wells to the transitional wet meadow zone, and six wells to the emergent zone (Appendix C). Of 59 species encountered at Roundup and Island lakes during the 1989 field season, there were 23 in the emergent zone, 30 in the wet meadow zone, and 38 in the upland zone.

The General Linear Models procedure for analysis of variance for 1989 soil series data indicated that depth to water table ($F_{4,147}$ = 47.70, prob > F = 0.0001) and soil moisture content ($F_{4,147}$ = 25.49, prob > F = 0.0001) were significant variables (Table 10). Hydric and upland soils were clearly distinguished by depth to water table, but overlapped for soil moisture content (Table 11). Depth to water table ranged from 46.3 cm for sites within the hydric Marlake series to 173.4 cm for the upland Ipage series. Depth to water table generally increased when moving from hydric to upland soils for all well lines at Roundup and Island lakes

(Figures 4-9). Soil moisture means ranged from 1.2% for the Ipage series to 25.9% for the Marlake soil series. Means of environmental parameters at individual well sites are found in Appendix D.

The General Linear Models procedure for analysis of variance for 1989 vegetation zones likewise indicated that depth to water table ($F_{2,149}$ = 88.10, prob > F = 0.0001) and soil moisture content ($F_{2,149}$ = 54.76, prob > F = 0.0001) were significant variables (Table 12). Duncan's multiple range tests of the parameters indicated that zones were significantly different from one another. Within vegetation zones, mean depth to water table ranged from 46.3 cm in the emergent zone to 132.9 cm in the upland zone (Table 13). Soil moisture content ranged from a mean of 4.2% in the upland zone to 25.9% in the emergent zone.

DISCUSSION

Applicability of the Unified Federal Method

The purpose of the unified federal method is to provide guidelines for determining whether an area is a jurisdictional wetland, and to delineate the upper wetland boundary (Federal Interagency Committee for Wetland Delineation 1989:1). Despite the care in assembling these guidelines, the unified federal method accepts two premises that could have repercussions for wetlands in both the Sandhills and other regions if they were erroneous. First, the unified federal method uses one-time assessments to determine wetland boundaries, without regard to seasonal or interannual changes in vegetation composition. To our knowledge, this premise has never been tested. Secondly, soil and vegetation data generally are expected to be congruent. In fact, Scott et al. (1989) examined some 38 hydric and 26 upland soils and reported that hydric soils generally supported wetland plants and upland soils supported upland vegetation, with very few exceptions. Unfortunately, because hydric characteristics are difficult to identify in Entisols, an Entisol pedon could meet the wetland hydrology criterion but still be misidentified if field indicators were not apparent. Thus, the potential for mistakes when establishing wetland boundaries in Entisols is great. These two premises will be discussed individually, in light of our findings.

First, regarding one-time assessments, our weekly calculations for the 1989 growing season showed little seasonal variation in prevalence indices. Although cover increased over time, relative vegetation composition changed very little through the 1989 growing season; species that were dominant in May likewise were dominant in August. Our results indicate that the premise behind one-time assessments of wetland boundaries is valid with regard to vegetation of Sandhill lakes and wetlands. However, changes do occur in hydrology during the growing season (see Appendices G and H). Thus, one-time assessments of wetland boundaries must be approached with caution when measuring hydrology.

Second, regarding the congruence between soil and vegetation data, quadrats of the four hydric soils in 1988 primarily supported wetland vegetation, whereas quadrats of the three upland soils mainly supported upland species. There also was a good correspondence between hydric soils and wetland vegetation in 1989. Five Entisols were encountered in our study, of which three were classified as upland and two were hydric (refer to taxonomic classes with "ent" suffix, Table 2). Soil and vegetation data were congruent for all Entisols except the Els, which suggests that the unified federal method was reliable for distinguishing between wetland and upland Entisols in the Sandhills. Overall, we found that soil and vegetation data gave identical results; however, there were two exceptions.

Two putative upland soils did not consistently have vegetation whose prevalence indices indicated predominantly upland species. Both the Dailey soils sampled in 1988 and the Els soils sampled around some lakes in 1988 and 1989 were dominated by wetland species. Did these series meet the wetland hydrology criterion? If not, then what might explain the predominance of wetland vegetation in quadrats of the Els and Dailey series? We offer several explanations for why these soils were not associated with upland vegetation. For ease of discussion, we have addressed the Els and Dailey soils separately.

The Dailey Series

Before asking if the Dailey series met the wetland hydrology criterion, we must address a potential shortcoming in our sampling design. More specifically, was the Dailey series sampled sufficiently? Soils in our study were not sampled uniformly because transect endpoints were selected using wetland and upland plant indicators rather than soils, as prescribed by the unified federal method. Although vegetation data for the Dailey series were collected from only 12 quadrats at a single site (i.e., Gimlet Lake), we nevertheless feel that the prevalence index accurately represented the vegetation composition at Gimlet Lake.

We believe that quadrats within the Dailey series, a Mollisol, met the wetland hydrology criterion because site hydrology had been altered. Results for the Dailey series were atypical for an upland soil because it was adjacent to a lake that was dredged approximately one year prior to our study. Disturbed sites create special problems when using the unified federal method (Federal Interagency Committee for Wetland Delineation 1989:50-55). Compatibility of vegetation and soil data previously was questionable when working with disturbed sites. While testing the predecessor of the unified federal method, Erickson and Leslie (1986) found that quadrats within the hydric Tryon series supported primarily upland vegetation (PI = 3.31, N = 40) at sites around Island Lake that were recently grazed. Similarly, both the nonhydric Rincon and hydric Alviso soils in California supported atypical vegetation communities when disturbed (Eicher 1988). Most invading ruderal plants associated with disturbance are classified as "facultative" species because they occur across broad environmental conditions; such species can make upland communities appear wetter and wetland communities appear drier when calculating prevalence indices (Scott et al. 1989:57).

The Els Series

Why did quadrats of the Els series support primarily wetland vegetation on occasions? Again, we first examine our sampling design. Els soils were sampled adequately in 1986 (N = 70) and 1988 (N = 129), and indicated primarily upland vegetation (PI = 3.82 and 3.30, respectively). Undersampling may have occurred when prevalence indices were calculated for individual lakes in 1988; three sites were dominated by wetland vegetation (Blue Lake: PI = 2.34, N = 6; Crane Lake: PI = 2.98, N = 13; Goose Lake: PI = 2.91, N = 10) (Appendix B). In 1988, soil pedons at every site were not examined; thus, the soils could have been misclassified. However, individual pedons were examined and classified by a soil scientist in 1989; those belonging to the Els series did support predominantly wetland vegetation (PI = 2.71, N = 112). Thus, we conclude that neither undersampling nor misidentification affected results compiled for the Els series. Likewise, disturbance was not documented at any sites with Els soils in 1988 or 1989.

Did individual Els pedons meet the wetland hydrology criterion as described by the unified federal method? A mean depth to water table of 129.2 cm was much greater than the recommended 45.7 cm (18.0 in) and mean soil moisture content was relatively low (5.3%) (see Table 11). Given these environmental measurements, we initially would conclude that these sites did not meet the wetland hydrology criterion. Yet, even though the presence of wetland vegetation does not necessarily indicate hydric conditions, quadrats within the Els series supported primarily wetland vegetation at three of the four well sites where it was found (Appendices E and F). In addition, our 1989 study area was fairly pristine, with no evidence of disturbance. Hence, we deemed it necessary to closely examine the legal description of the Els soil series for hydric characteristics.

By definition, hydric soils in an undrained state are "saturated, flooded, or ponded long enough during the growing season to develop anaerobic conditions that favor the growth and regeneration of hydrophytic vegetation" (Soil Conservation Service 1985:1). Entisols that are saturated with groundwater (i.e., having an aquic or peraquic moisture regime) are truly hydric unless effectively drained (Federal Interagency Committee for Wetland Delineation 1989:58). However, many hydric Entisols are difficult to identify because they lack characteristic field indicators. In particular, Entisols composed of loamy fine sand or coarser textures within 51.0 cm (20.0 in) of the surface may contain insufficient clays and organics needed to develop hydric soil colors, and hence can be misidentified (Federal Interagency Committee for Wetland Delineation 1989:58). Soils usually are considered hydric only if they have a matrix chroma of 2 or less in mottled soils, or else 1 or less in unmottled soils (Federal Interagency Committee for Wetland Delineation 1989:14). Coarse-textured Entisols, though, are exempted from this generalization if they have a hue between 10YR and 10Y in addition to distinct mottling; a chroma of 3 or less is then acceptable and the soil can be designated as hydric (Federal Interagency Committee for Wetland Delineation 1989:58).

The Soil Conservation Service (undated) reported that the Els series met the color morphology of Psammaquents, but did not meet the saturation requirements of the Aquent suborder, as defined by the Soil Conservation Service (1975). Thus, the series was placed into the subgroup Aquic Ustipsamment. Although the Aquic Ustipsamments are not considered hydric by the Soil Conservation Service (1975), they are saturated with water at some time of the year and often have mottles of low or high chroma within 1 m of the soil surface, which meets the criteria for hydric soils reported by the Federal Interagency Committee for Wetland Delineation (1989:6). In addition to the Els series, two other upland soils (i.e., Ipage and Wildhorse) are described as having aquic regimes; however, neither of these soils supported wetland vegetation in either 1988 or 1989.

The Els series is defined as somewhat poorly drained soils that formed in aeolian and alluvial sands on depressed areas and valleys of the Sandhills, and on foot slopes and stream terraces draining the Sandhills (Appendix A). The series description reports a hue of 10YR in the A (0 to 18 cm), AC (18 to 36 cm), and C (36 to 152 cm) horizons, and presence of mottles in the AC and C horizons. Chroma varies between 1 and 2 in the A horizon to 2 and 3 in the C horizon (Soil Conservation Service, undated). These characteristics appear to fit stipulations given by the Federal Interagency Committee for Wetland Delineation (1989).

However, the possibility also exists that the Els series is neither hydric nor upland but rather is transitional in nature. Inherent difficulties are present when creating dichotomous classifications for soils (Scott et al. 1989). Because the concept of a soil "series" is artificial, it may allow similar but not identical soil pedons to be combined. Thus, it is plausible that the Els series inadvertently is composed of both hydric and upland pedons. If so, then this could explain why Els quadrats supported upland vegetation in 1986, both upland and wetland plants in 1988, and wetland vegetation in 1989. Other researchers using the unified federal method or variations of the method have obtained similar results. Hubbard et al. (1988) reported that vegetation composition differed along a topographic gradient within the hydric Vallers series in South Dakota. Relative amounts of wetland vegetation increased significantly as elevation decreased. Scott et al. (1989:49) stated that sites with intermediate vegetation often had "borderline" soils between upland and wetland sites. They further noted that the original premise behind the unified federal method is strengthened by such exceptions to an exact correspondence between vegetation and soils. Unfortunately, if some soils actually are transitional between upland and hydric, then the delineation of wetlands with these soils must rely on vegetation and hydrological criteria.

The Wetland Hydrology Criterion

The Environmental Protection Agency expressed concern as to whether seven days of saturation and 45.7 cm (18.0 in) depth to water table with dry soil surfaces were valid indicators of the wetland hydrology criterion. We do not have a clear cut answer to this question. A definition of soil saturation is not given in the manual because variations in soil composition make such a definition difficult if not impossible to draft. Both the Els and Ipage upland soils contained less than 6% water, compared to more than 10% water for the hydric soils. Statistically, mean soil moisture contents for the hydric Tryon series (10.9%) were not different from that of the upland Els soil (5.3%); however, roughly a 5% difference in moisture could be biologically significant for plants growing in these soils. Depth to water table was greater than 45.7 cm for the upland soils, but the same was true of all hydric soils (see Table 11). The concern about depth to water table seems unfounded in the context of our study. Indeed, our data suggest that depths as great as 75.0 cm (29.5 in) would be indicative of wetland conditions in the Sandhills.

Finally, the Environmental Protection Agency questioned the validity of using indirect estimates of hydrology to assess the wetland hydrology criterion. Difficulties with estimating hydrology indirectly also have been recognized by the unified federal method. The Federal Interagency Committee for Wetland Delineation (1989:17) specifically cautions that assessments using field indicators are subjective and may prove "technically inaccurate" when delineating wetland boundaries.

We examined how indirect and direct measures of wetland hydrology corresponded to vegetation composition at our study area. Our 1988 and 1989 analysis of variance models examined a surrogate hydrology parameter, referred to in the text as "transect location" (i.e., position along lake and shore; see Tables 4 and 6). We assumed that transect location reflected local hydrology because differences in the amount of time a wetland is flooded or influenced by groundwater is a function of elevation (LaBaugh 1986, Winter 1989). Both transect location and soil series identity affected vegetation composition in 1988 and 1989, but in both years soil was more important than transect location (see Tables 4 and 6).

Our 1989 analyses indicated that vegetation composition, represented by vegetation zones, was related to both the direct (i.e., depth to water table) and indirect measures of hydrology (i.e., soil moisture content). Depth to water table clearly distinguished among quadrats within hydric and upland series; however, hydric and upland soils with similar textures were not readily separated by soil moisture content. Our data indicate that vegetation and hydrology corresponded more closely to one another than soil series identity and hydrology. Although an indirect estimate of the wetland hydrology criterion would be reasonably accurate when vegetation and soil data are comparable, as in distinctly wetland or upland sites, indirectly estimating the wetland hydrology criterion could create problems when delineating the boundary between wetland and upland habitats.

RECOMMENDATIONS

Our data imply that the Els soil series could be wrongly classified as an upland soil. The Els series has characteristics that fall within guidelines for hydric soils (Federal Interagency Committee for Wetland Delineation 1989), and the soils often support a predominance of wetland vegetation. However, it also is plausible that the series is a transitional soil that is neither truly hydric nor truly upland. Either way, though, we suggest that the Els soil receive consideration for reclassification by the Soil Conservation Service.

For the most part, the unified federal method would be useful in delineating wetlands of the Nebraska Sandhills, despite the number of Entisols encountered. However, we recognize that indirectly estimating the wetland hydrology criterion could cause discrepancies when delineating boundaries of Sandhill wetlands. Procedures that incorporate direct measurements of hydrology into onsite delineation processes would be very useful, particularly if transitional soils were encountered. Efforts also should be made to define more precisely some indirect estimates of the wetland hydrology criterion. For example, "soil saturation" for different textures of soils could be quantified within some acceptable range. Requiring the water table to be within 30.0 cm (18.0 in) of the surface might indicate hydric conditions for some substrates, but certainly not for our sandy soils, where 75.0 cm could indicate hydric conditions.

The ideal scenario would be to quantify and weight direct measurements of hydrology, much like calculating prevalence indices for vegetation composition. An index of hydrology could then be compared directly to vegetation and soil parameters. Although the idea of developing an index of hydrology may be premature, such procedures eventually would be invaluable particularly in the Nebraska Sandhills. Here, impacts to hydrology via groundwater depletion are the primary cause of wetland habitat destruction. The ability to incorporate hydrology indices into onsite assessment procedures potentially could provide the most sensitive means for delineating boundaries of Sandhill wetlands.

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Table 1. Definitions of wetland indicator groups assigned to plant species by Reed (1988)

Indicator Group	Definition
Obligate	occur almost always (>99% probability) in wetlands under natural conditions
Facultative Wetland	usually occur in wetlands (67-99% probability) but occasionally are found in nonwetlands
Facultative	as likely to occur in wetlands or nonwetlands (34-66% probability)
Facultative Upland	usually occur in nonwetlands (67-99% probability) but occasionally are found in wetlands (1-33% probability)
Upland	occur almost always (>99% probability) in nonwetlands under natural conditions

Table 2. Soil series and their taxonomic classes (Soil Conservation Service, undated); Soil Conservation Service (1985) hydric soils are denoted by *

Soil Series	Taxonomic Class
Dailey	Sandy, mixed, mesic Torriorthentic Haplustolls
Els	Mixed, mesic Aquic Ustipsamments
*Hoffland	Sandy, mesic Typic Calciaquolls
Ipage	Mixed, mesic Aquic Ustipsamments
*Loup	Sandy, mixed, mesic Typic Haplaquolls
*Marlake	Sandy, mixed, mesic Mollic Fluvaquents
*Tryon	Mixed, mesic Typic Psammaquents
Valentine	Mixed, mesic Typic Ustipsamments
Wildhorse	Sandy, mixed, mesic Typic Haplaquepts

Table 3. The number of plant species supported by quadrats within each soil series in 1986, 1988, and 1989 studies; Soil Conservation Service (1985) hydric soils are denoted by *

	1986		1988		1989	
Soil Series	N[a]	species	N	species	N	species
*Marlake	109	56	123	61	168	23
*Hoffland	40	44	26	35	28	12
*Loup	40	43	13	36	--[b]	--
*Tryon	40	38	173	100	196	31
Els	70	43	129	85	112	31
Dailey	--	--	12	27	--	--
Wildhorse	--	--	34	47	--	--
Valentine	40	27	69	62	--	--
Ipage	--	--	71	62	28	9
Subtotals:						
Hydric soils	229	--	335	117	392	44
Upland soils	110	--	315	109	140	36
TOTAL	339	132[c]	650	159	532	59

[a] Number of quadrats sampled.
[b] Data not available.
[c] Subtotals and total account for species overlap among soil series.

Table 4. General Linear Models procedure for analysis of variance for soil, lake, and shore effects on prevalence indices in 1988

Dependent variable: Prevalence Index

Source	df	SS	Mean Square	F Value	Pr > F
Model	33	555.09	16.82	54.65	0.0001
Error	615	189.30	0.31		
Corrected	648	744.39			

Source	df	Type I	Mean Square	F Value	Pr > F
SOIL	8	515.33	64.42	209.27	0.0001
LAKE(SHORE)	25	39.76	1.59	5.17	0.0001

Source	df	Type III	Mean Square	F Value	Pr > F
SOIL	8	477.06	59.63	193.73	0.0001
LAKE(SHORE)	25	39.76	1.59	5.17	0.0001

Table 5. Duncan's multiple range test for differences among prevalence indices calculated for soil series of quadrats along Sandhill lakes in 1988; means in the same letter group are not significantly different; Soil Conservation Service (1985) hydric soils are denoted by *

Soil	N	Mean	Group
Valentine	69	3.99	A
Wildhorse	34	3.86	A
Ipage	71	3.82	A
Els	129	3.30	B
Dailey	12	2.91	C
*Tryon	173	2.40	D
*Loup	13	2.47	D
*Hoffland	26	2.41	D
*Marlake	122	1.39	E

Table 6. General Linear Models procedure for analysis of variance for soil, lake, and shore effects on prevalence index in 1989

Dependent variable: Prevalence Index

Source	df	SS	Mean Square	F Value	Pr > F
Model	7	243.92	34.85	199.93	0.0001
Error	524	91.33	0.17		
Corrected	531	335.24			

Source	df	Type I	Mean Square	F Value	Pr > F
SOIL	4	225.01	56.25	322.76	0.0001
LAKE(SHORE)	3	18.91	18.91	36.16	0.0001

Source	df	Type III	Mean Square	F Value	Pr > F
SOIL	4	226.54	56.63	324.95	0.0001
LAKE(SHORE)	3	18.91	18.91	36.16	0.0001

Table 7. Duncan's multiple range test for differences among prevalence indices calculated for soil series of quadrats along groundwater wells in 1989; means in the same letter group are not significantly different; Soil Conservation Service (1985) hydric soils are denoted by *

Soil	N	Mean	Group
Ipage	28	3.51	A
Els	112	2.71	B
*Tryon	196	2.01	C
*Hoffland	28	1.80	C
*Marlake	168	1.21	D

Table 8. Duncan's multiple range test for differences among prevalence indices calculated weekly for soil series of quadrats at groundwater wells in 1989; means in the same letter group are not significantly different; Soil Conservation Service (1985) hydric soils are denoted by *

Soil	N	Mean	Group
19-21 June 1989 ($F_{4,75}$ = 31.27, prob > F = 0.0001)			
Ipage	4	3.21	A
Els	16	2.70	B
*Tryon	28	2.00	C
*Hoffland	4	1.57	C, D
*Marlake	24	1.21	D
2-4 July 1989 ($F_{4,75}$ = 30.63, prob > F = 0.0001)			
Ipage	4	3.33	A
Els	16	2.75	B
*Tryon	28	2.01	C
*Hoffland	4	1.80	C
*Marlake	24	1.21	D
18-20 July 1989 ($F_{4,75}$ = 52.47, prob > F = 0.0001)			
Ipage	4	3.65	A
Els	16	2.60	B
*Tryon	28	1.99	C
*Hoffland	4	1.72	C
*Marlake	24	1.20	D
24-26 July 1989 ($F_{4,75}$ = 43.58, prob > F = 0.0001)			
Ipage	4	3.65	A
Els	16	2.63	B
*Tryon	28	2.00	C
*Hoffland	4	1.89	C
*Marlake	24	1.21	D

Table 8. (continued)

Soil	N	Mean	Group
1-3 August 1989 ($F_{4,75}$ = 40.81, prob > F = 0.0001)			
Ipage	4	3.56	A
Els	16	2.68	B
*Tryon	28	1.96	C
*Hoffland	4	1.75	C
*Marlake	24	1.21	D
7-9 August 1989 ($F_{4,75}$ = 35.38, prob > F = 0.0001)			
Ipage	4	3.64	A
Els	16	2.83	B
*Tryon	28	2.07	C
*Hoffland	4	1.80	C
*Marlake	24	1.21	D
13-15 August 1989 ($F_{4,75}$ = 36.28, prob > F = 0.0001)			
Ipage	4	3.55	A
Els	16	2.64	B
*Tryon	28	2.07	C
*Hoffland	4	2.04	C
*Marlake	24	1.21	D

Table 9. A comparison of 1986 (Erickson and Leslie 1986), 1988, and 1989 data using Duncan's multiple range tests to indicate differences among prevalence indices for hydric and upland soil series of Sandhill Lakes; means in the same letter group are not significantly different; Soil Conservation Service (1985) hydric soils are denoted by *

	1986			1988			1989		
Soil	N	Mean	Group	N	Mean	Group	N	Mean	Group
Valentine	40	4.27	A	69	3.99	A	--[a]	--	--
Wildhorse	--	--	--	34	3.86	A	--	--	--
Ipage	--	--	--	71	3.82	A	28	3.51	A
Els	70	3.83	B	129	3.30	B	112	2.71	B
Dailey	--	--	--	12	2.91	C	--	--	--
*Tryon	40	3.31	C	173	2.40	D	196	2.01	C
*Loup	40	2.47	D	13	2.47	D	--	--	--
*Hoffland	40	2.40	D	26	2.41	D	28	1.80	C
*Marlake	109	1.58	E	122	1.39	E	168	1.21	D

[a] Data not available.

Table 10. General Linear Models procedure for analysis of variance for soil series effects on environmental parameters in 1989; significant variables (i.e., with significance levels less than 0.0005) are denoted by *

Parameters	$F_{4,147}$	Prob > F	R^2
Depth to water table	47.70	0.0001*	0.56
Soil moisture content	25.49	0.0001*	0.41
pH	2.07	0.0833	0.05
Specific conductance	1.26	0.2866	0.03

Table 11. Duncan's multiple range test for differences among environmental parameter means calculated for soil series in 1989; means in the same letter group are not significantly different; Soil Conservation Service (1985) hydric soils are denoted by *

Soil	N	Mean	Group
		Depth to Water Table (cm)	
Ipage	8	173.4	A
Els	32	129.2	B
*Tryon	56	73.9	C
*Hoffland	8	68.6	C, D
*Marlake	48	46.3	D
		Soil Moisture Content (%)	
*Marlake	48	25.9	A
*Hoffland	8	15.8	B
*Tryon	56	10.9	B, C
Els	32	5.3	C, D
Ipage	8	1.2	D
		pH	
*Tryon	56	7.20	A
*Hoffland	8	7.20	A
Els	32	6.93	A, B
*Marlake	48	6.76	A, B
Ipage	8	6.02	B
		Specific Conductance (μS/cm)	
Els	32	1191	A
*Tryon	56	1187	A
*Marlake	48	888	A
*Hoffland	8	672	A
Ipage	8	115	A

Table 12. General Linear Models procedure for analysis of variance for effects of vegetation zones on environmental parameters in 1989; significant variables (i.e., with significance levels less than 0.0005) are denoted by *

Parameters	$F_{2,149}$	Prob > F	R^2
Depth to water table	88.10	0.0001*	0.54
Soil moisture content	54.76	0.0001*	0.42
pH	1.92	0.1504	0.03
Specific conductance	0.85	0.4284	0.01

Table 13. Duncan's multiple range test for differences among environmental parameter means calculated for vegetation zones in 1989; means in the same letter group are not significantly different

Vegetation Zone	N	Mean	Group
	Depth to Water Table (cm)		
Upland	48	132.9	A
Wet Meadow	56	68.4	B
Emergent	48	46.3	C
	Soil Moisture Content (%)		
Emergent	48	25.9	A
Wet Meadow	56	12.7	B
Upland	48	4.2	C
	pH		
Wet Meadow	56	7.20	A
Upland	48	6.82	A
Emergent	48	6.76	A
	Specific Conductance (μS/cm)		
Wet Meadow	56	1214	A
Upland	48	894	A
Emergent	48	888	A

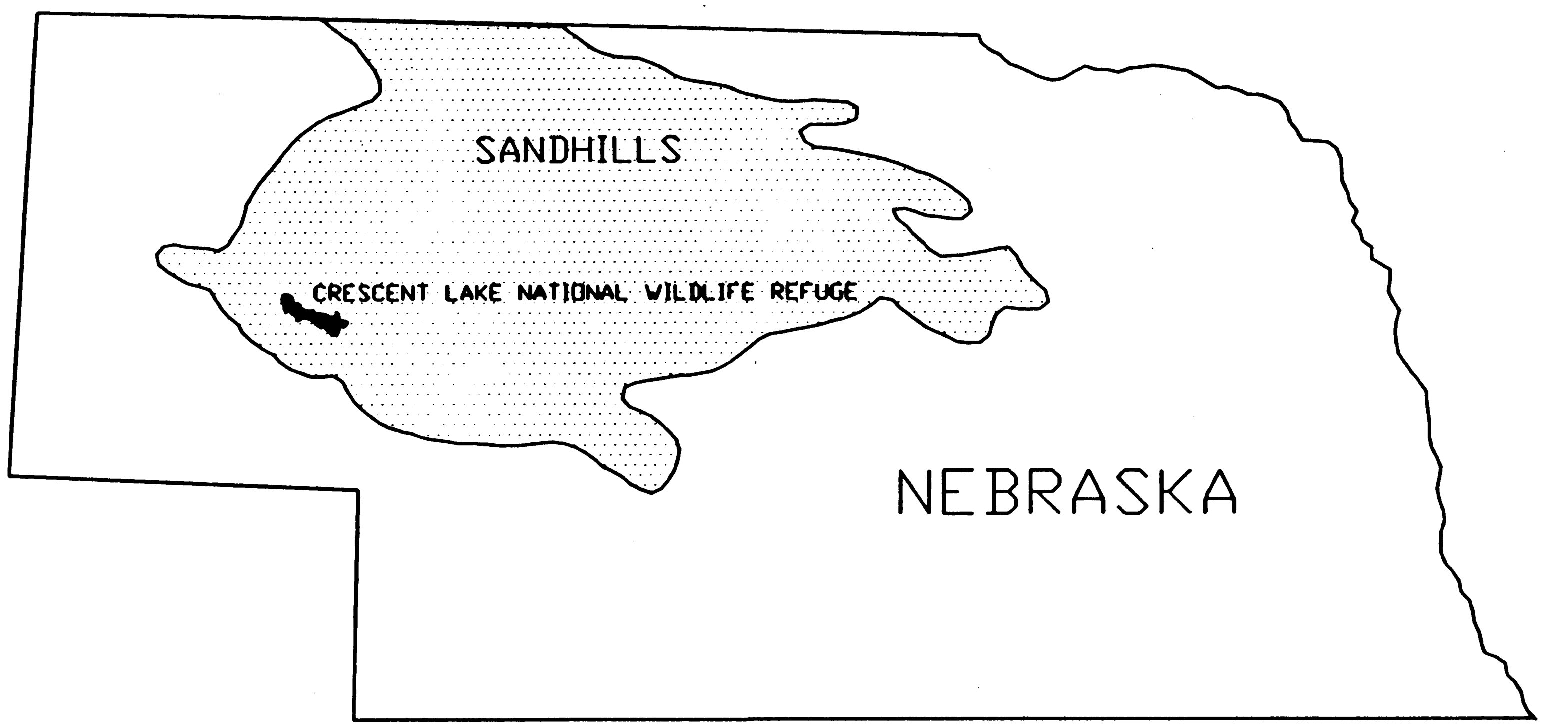

Figure 1. Location of the Sandhills of Nebraska and Crescent Lake National Wildlife Refuge within the Sandhills

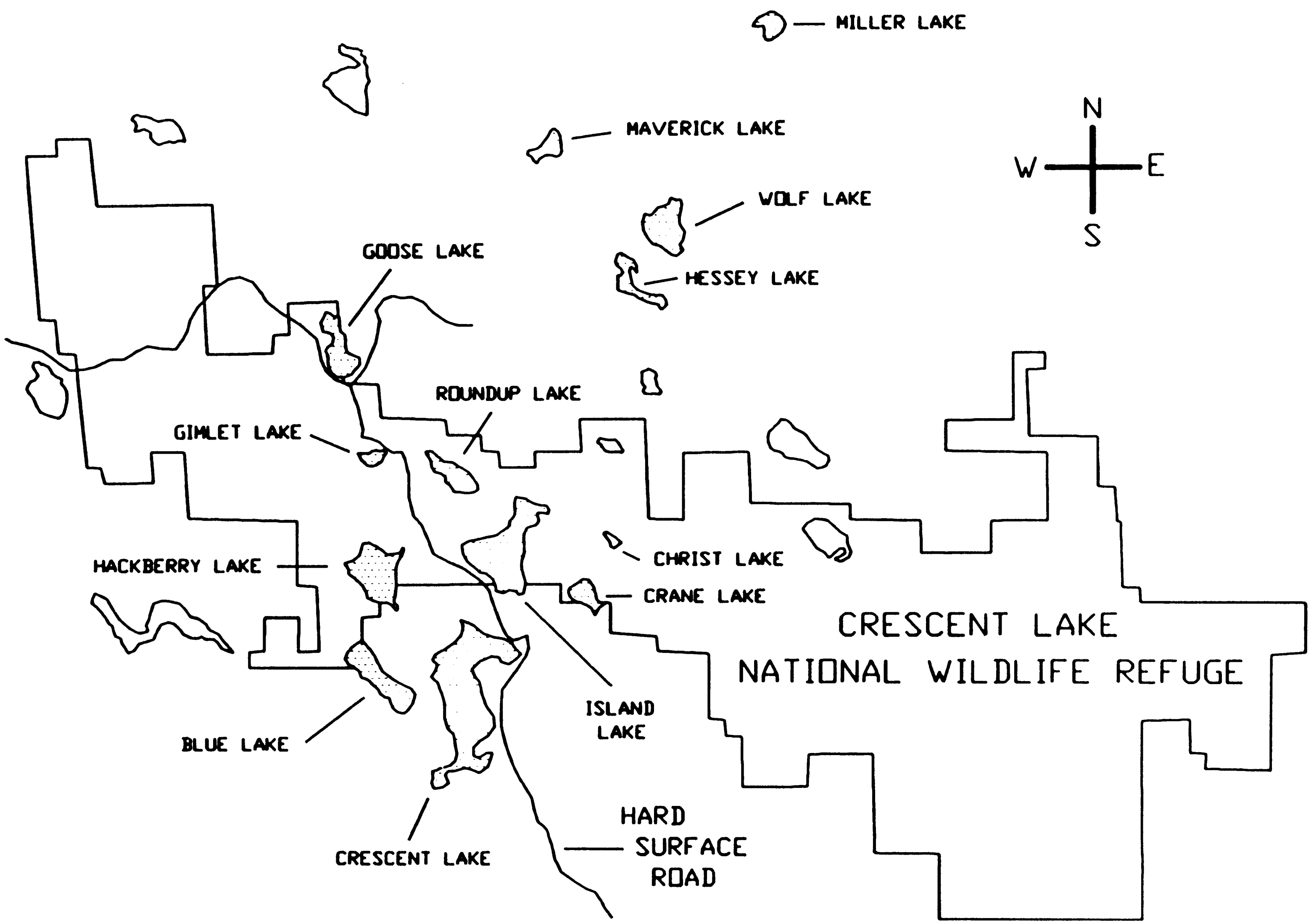

Figure 2. Location of 13 lakes in and adjacent to Crescent Lake National Wildlife Refuge that were sampled in 1988

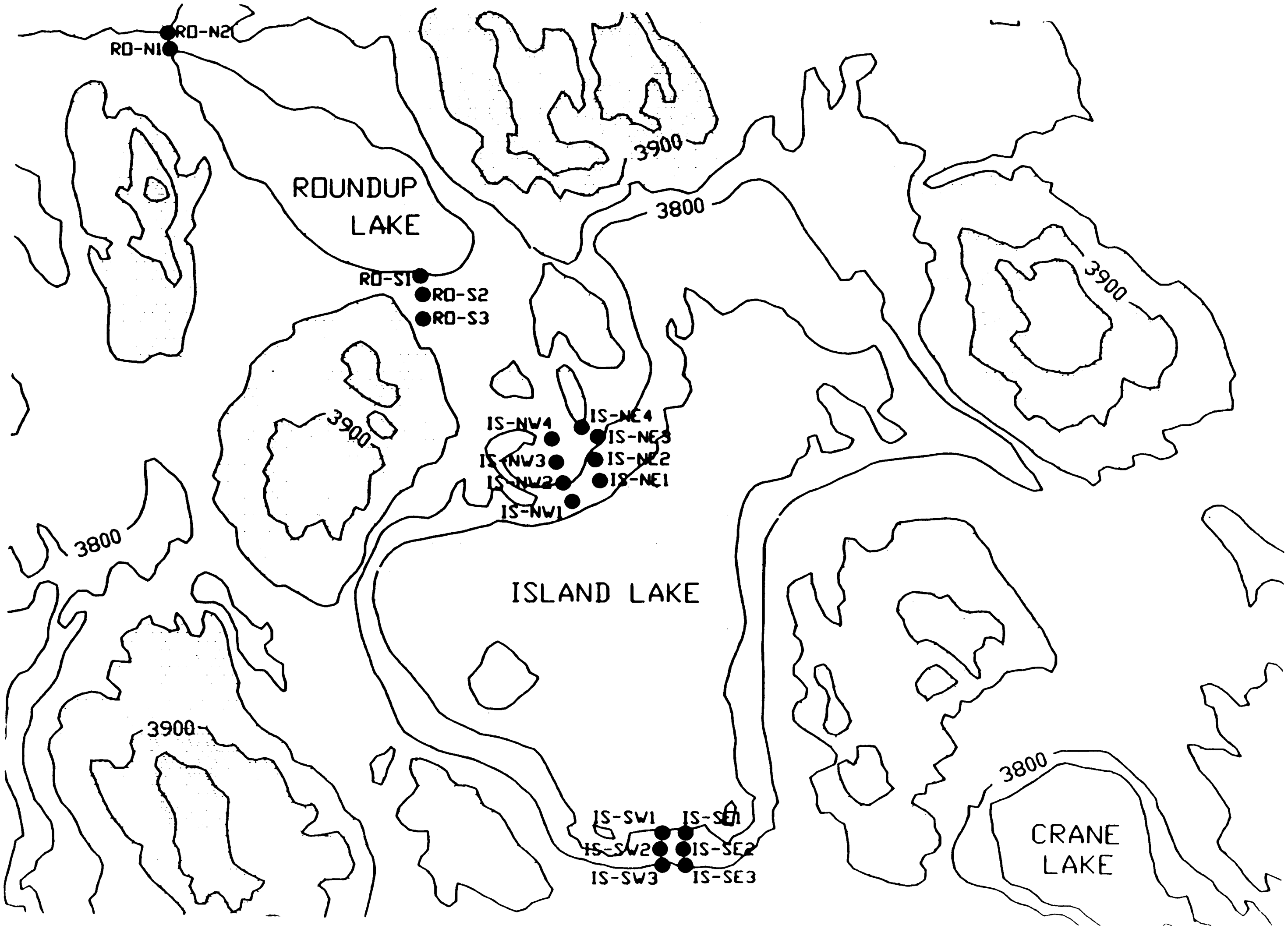

Figure 3. Location of groundwater well lines around Roundup and Island lakes, Crescent Lake National Wildlife Refuge

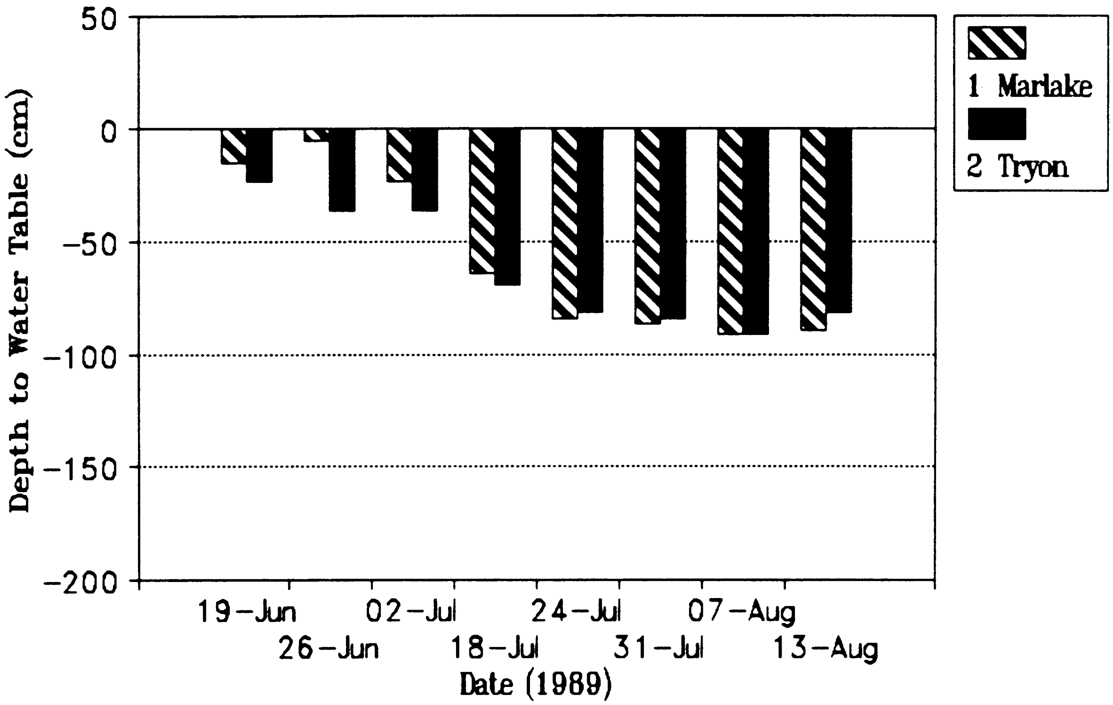

Figure 4. Depth to water table in 1989 by soil series for the groundwater well line along the north shore of Roundup Lake

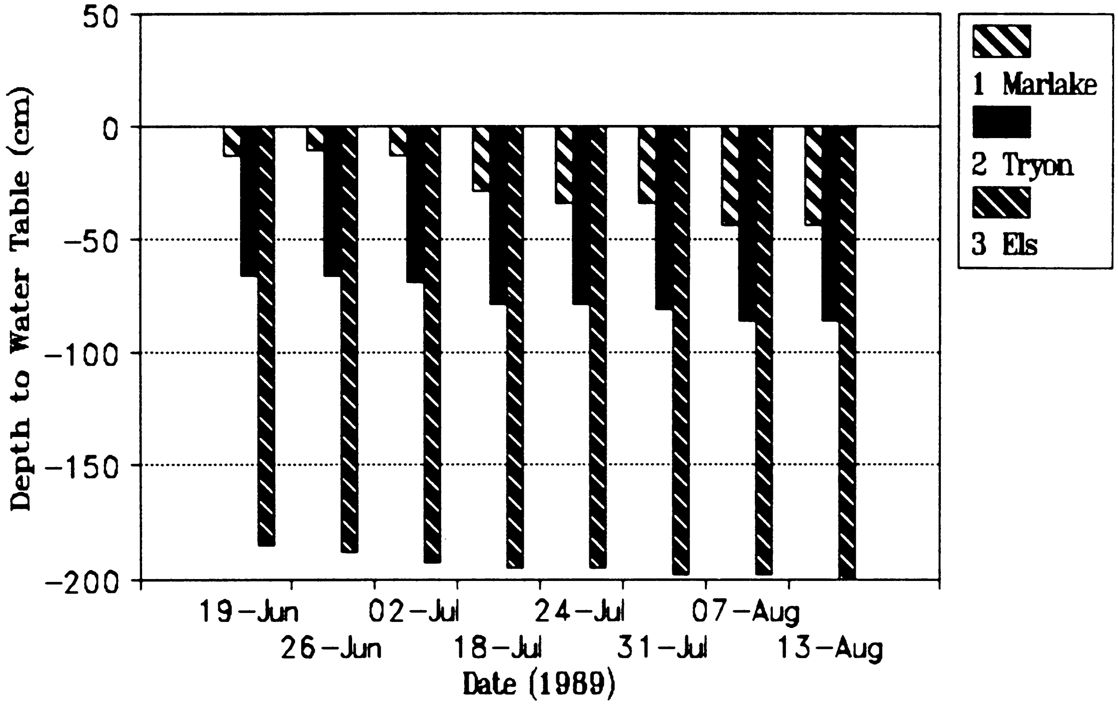

Figure 5. Depth to water table in 1989 by soil series for the groundwater well line along the south shore of Roundup Lake

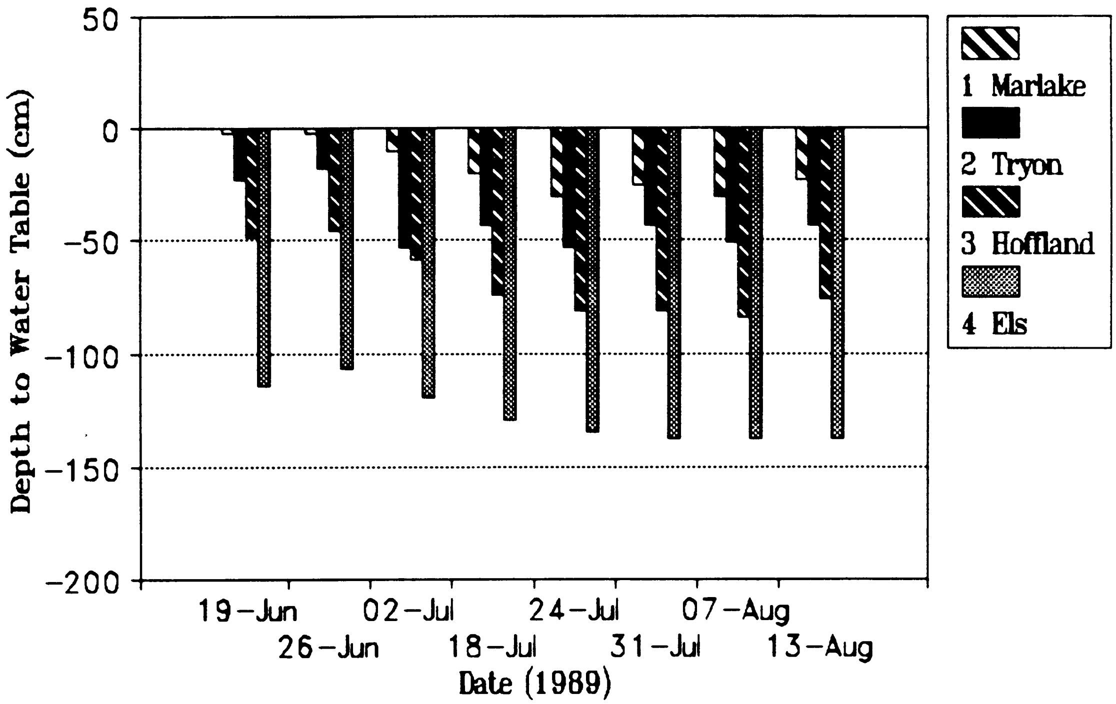

Figure 6. Depth to water table in 1989 by soil series for the west groundwater well line along the north shore of Island Lake

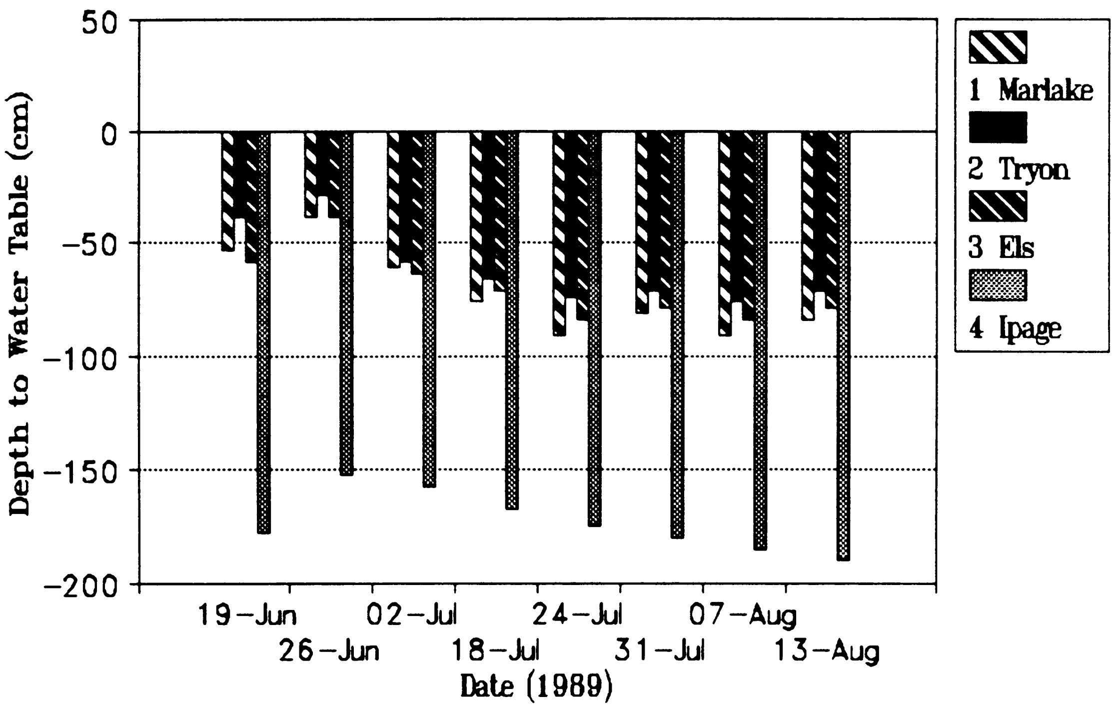

Figure 7. Depth to water table in 1989 by soil series for the east groundwater well line along the north shore of Island Lake

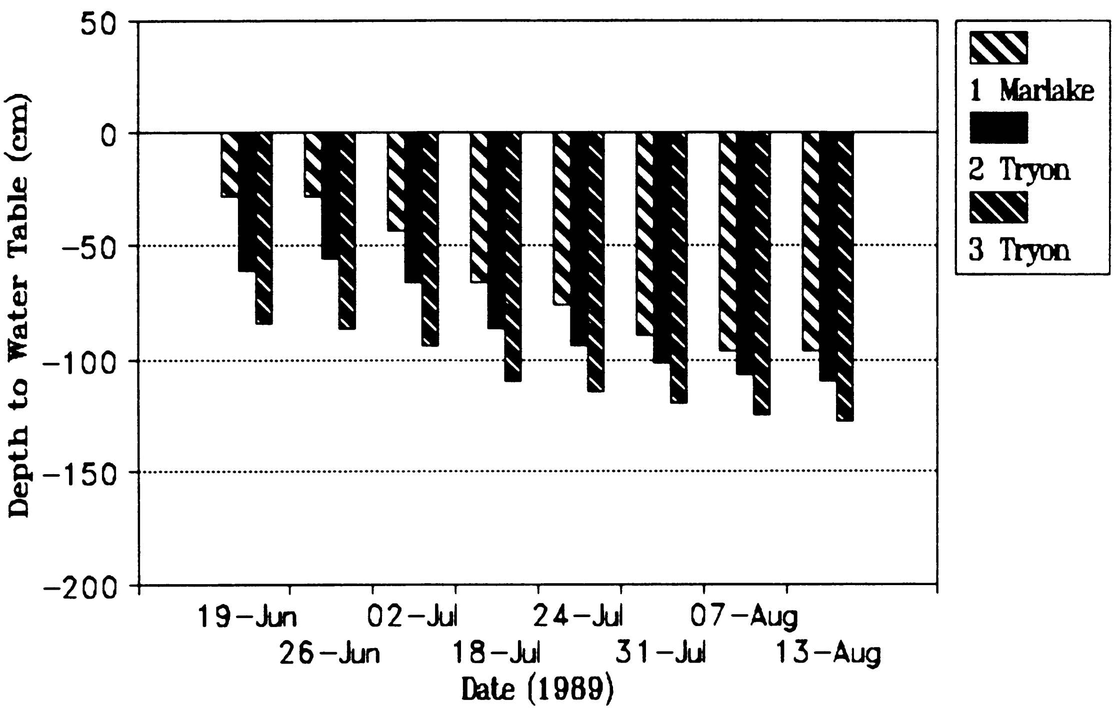

Figure 8. Depth to water table in 1989 by soil series for the west groundwater well line along the south shore of Island Lake

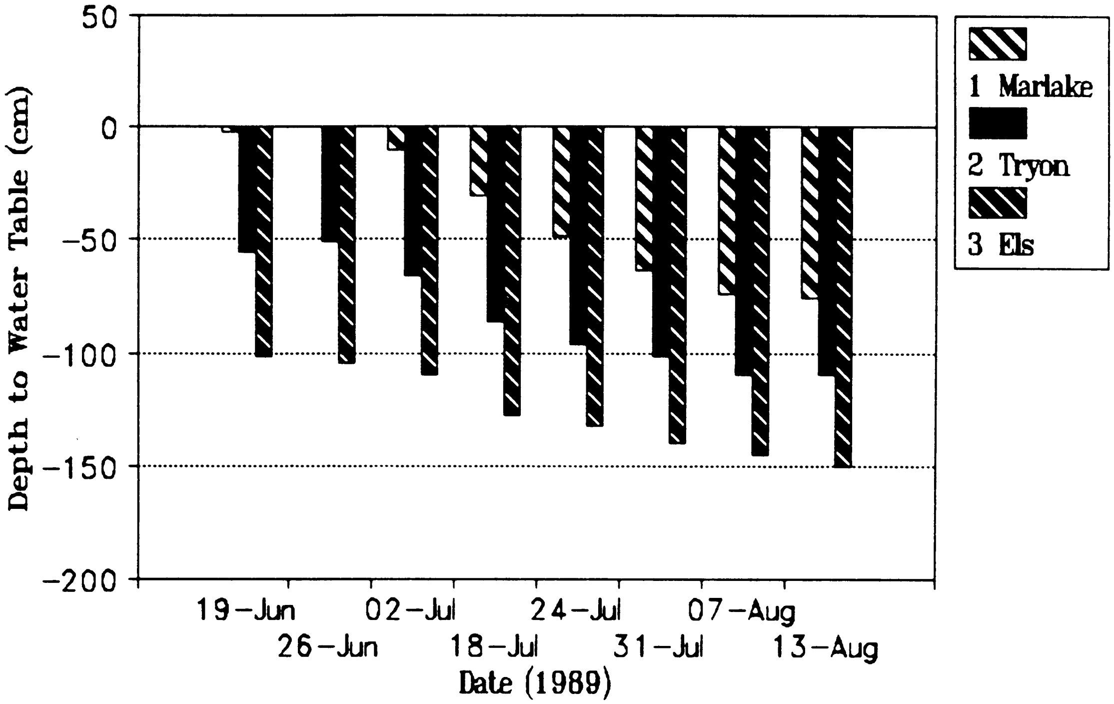

Figure 9. Depth to water table in 1989 by soil series for the east groundwater well line along the south shore of Island Lake

APPENDIX A

Description of soil series; taxonomic class descriptions are taken from Soil Conservation Service (1975) and series descriptions are taken from Soil Conservation Service (undated); Soil Conservation Service (1985) hydric soils are denoted by *

DAILEY (Sandy, mixed, mesic Torriorthentic Haplustoll): Ustolls are more or less freely drained Mollisols. Most rainfall comes during the growing season but often is erratic. Drought is frequent and may be severe. Ustolls have a cambic horizon or a horizon with slightly altered parent material below the mollic epipedon. Most also have a horizon in which carbonates or soluble salts have accumulated. Haplustolls are mainly in late-Pleistocene or Holocene deposits or on surfaces of comparable age. Vegetation is dominantly grasses and forbs. Torriorthentic Haplustolls are soils that are drier than the typic, and either are calcareous in the major part of the epipedon or lack a cambic horizon.

The Dailey series is very deep and somewhat excessively drained soils, with a 0-12% slope. The soil formed in sandy aeolian sediment; surface soil is greyish-brown loamy sand 41 cm thick, and subsoil is pale brown loamy sand 112 cm thick. Runoff is slow and permeability is rapid. Mean annual precipitation is 41 cm, and mean annual temperature is 9^{o} C. Most acreage is used for pastureland, although some areas are irrigated. Distribution is eastern Colorado, western Nebraska, and Wyoming.

ELS (Mixed, mesic Aquic Ustipsamment): Psamments are Entisols in poorly graded (well sorted) sands of shifting or stabilized sand dunes. Age is recent to Pliocene, or older. Soils have a low water-holding capacity and when dry and bare, they are subject to blowing and drifting. Ustipsamments are Psamments with an ustic moisture regime (i.e., moisture usually is present only during the growing season). Soils are freely drained sands with mostly grass or savanna vegetation. Aquic Ustipsamments are saturated with water at some time of the year and have mottles of low or high chroma within 1 m of the soil surface.

The Els series occurs above Loup and Tryon and below Ipage series in the landscape. The series is a deep, poorly drained soil, with a 0-3% slope. The soil formed in aeolian and alluvial sands on depressed areas and valleys of the Sandhills and on foot slopes and stream terraces draining the Sandhills. The surface is greyish-brown fine sand 18 cm thick. The subsoil layer is light brownish-grey fine sand 18 cm thick. The substratum is light grey mottled fine sand. Runoff is slow and permeability is rapid. The water table ranges from 46 cm in wet years to 91 cm in dry years. Mean annual precipitation ranges from 36-69 cm, and mean annual temperature is 8-11^{o} C. Native vegetation is in grassland, and most land is used for hayland or range. However, some acreage is used for alfalfa, corn, grain sorghum, wheat, and introduced grasses. The series has a Nebraska Sandhills, Kansas, South Dakota, and Colorado distribution.

***HOFFLAND (Sandy, mesic Typic Calciaquoll):** Aquolls are Mollisols that are naturally wet. These soils have dominant low chroma and high contrast mottles below a black epipedon. They commonly develop in low places where water collects and stands, although some form on broad flats or seepy hillsides. Calciaquolls are Aquolls that have a shallow calcic or gypsic horizon.

The Hoffland series occurs above Marlake and below Els series in the landscape. The series is made of deep, poorly drained soils characterized by a 0-2% slope and a high calcium carbonate content. These soils formed in alluvial sediments in Sandhill valleys. The surface soil is grey and light brownish-grey fine sandy loam 28 cm thick. The substratum is 76 cm of light brownish-grey fine sand over 20 cm dark greyish-brown fine sandy loam over light grey fine sand. Runoff is slow or ponded, and permeability is rapid. Mean annual precipitation range is 38-46 cm, and mean annual temperature is 7-9^{o} C. Nearly all acreage is in native grass that is used for hayland and range. The series has a western Nebraska Sandhills distribution.

IPAGE (Mixed, mesic Aquic Ustipsamment): Psamments are Entisols in poorly graded (well sorted) sands of shifting or stabilized sand dunes. Age is recent to Pliocene, or older. Soils have a low water-holding capacity and when dry and bare, they are subject to blowing and drifting. Ustipsamments are Psamments with an ustic moisture regime (i.e., moisture usually is present only during the growing season). Soils are freely drained sands with mostly grass or savanna vegetation. Aquic Ustipsamments are saturated with water at some time of the year and have mottles of low or high chroma within 1 m of the soil surface.

The Ipage series occurs above Els, Loup, and Tryon, and below Valentine series in the landscape. The soil is deep and moderately well drained, with a 0-6% slope. The series formed in aeolian and alluvial sands on upland valleys and along stream terraces. The surface layer is dark greyish-brown sand 13 cm thick. The subsoil layer is greyish brown sand 15 cm thick. The substratum is pale brown sand and very pale brown and white sand over light grey coarse sand 109 cm thick. Runoff is slow and permeability is rapid. Mean annual precipitation range is 41-61 cm, and mean annual temperature is 8-11^{o} C. The native vegetation is grassland, and the soil is used principally as hayland and range. However, a small acreage is cultivated to corn and alfalfa; most of the corn acreage is irrigated. The series has a distribution from the Nebraska Sandhills to South Dakota.

***LOUP (Sandy, mixed, mesic Typic Haplaquoll):** Aquolls are naturally wet Mollisols with a vegetation of grasses, sedges, and forbs. Haplaquolls are soils with a black epipedon that grades into a gray or olive gray mottled cambic horizon.

The Loup series occurs above Marlake and below Els series in the landscape. The series is deep and nearly level, with a 0-2% slope. This poorly drained soil formed in loamy and sandy alluvium bottomlands and around marshes and lakes. The surface layer is calcareous, very dark grey, and dark grey fine sandy loam 25 cm thick. The subsurface layer is grey fine sand 10 cm thick. The substratum is 109 cm of light grey and greyish-brown fine sand over dark grey fine sandy loam. Overall organic matter content is high. Permeability is rapid and depth to the water table ranges from 15-30 cm. Mean annual precipitation ranges from 38-66 cm, and mean annual temperature is 7-12^{o} C. The soil is in native grass and is used for rangeland or hayland, but usually is too wet for farming. The soil has a Nebraska Sandhills, South Dakota, and Colorado distribution.

***MARLAKE (Sandy, mixed, mesic Mollic Fluvaquent):** Aquents are wet Entisols found where the soil is continuously saturated with water. Fluvaquents are found primarily in floodplains and deltas and have a relatively high content of organic carbon at considerable depths when compared to other wet mineral soils. Sediments are of Holocene age. Mollic Fluvaquents are identical to Mollisols in surface horizon, color, and other properties except they lack the thickness characteristic of a mollic epipedon. They have a high base saturation, and some are calcareous.

The Marlake series occurs below Hoffland, Loup, Tryon, Els, and Valentine series in the landscape. The soil is deep and nearly level, with a 0-1% slope. The series is a poorly drained soil formed in colluvial and alluvial sands that is located in depressions or basins on valley floors and in low areas bordering lakes and streams. The surface layer is dark grey loamy fine sand 18 cm thick. The subsoil is greyish-brown loamy sand with thin strata of sandy loam and sand 23 cm thick. The substratum is light grey mottled fine sand. Organic matter content is high. The soil usually is inundated during the growing season, and has a high permeability. Mean annual precipitation ranges from 43-58 cm, and mean annual temperature is 8-11^{o} C. The soil mostly is used as wildlife habitat; some areas are mowed in dry years for mulching materials. The series has a northcentral, central, and western Nebraska distribution.

***TRYON (Mixed, mesic Typic Psammaquent):** Psammaquents are Aquents with sandy texture and gray or mottled gray colors. The water table is at or near the surface of the soil for long periods unless artificially drained. Most have formed in late Pleistocene to recent sediments.

The Tryon series occurs above Marlake and below Els series in the landscape. The soil is deep, poorly drained, and has a 0-2% slope. This series formed in aeolian and alluvial sediments in Sandhill valley floors and on bottomlands of some major streams which drain the Sandhills. The surface layer is very dark brown loamy fine sand 13 cm thick. The subsurface layer is light brownish-grey loamy sand to grey fine sand 14-23 cm thick. The substratum is 104 cm of light brownish grey fine sand over 18 cm of black fine sandy loam over dark grey fine sand. Organic matter content is high, and permeability is rapid. Mean annual precipitation range is 36-61 cm, and mean annual temperature is 8-11^{o} C. The soil is suited to grazing or haying but is too wet for cultivation. The soil has a distribution that extends through the Nebraska Sandhills and central Great Plains.

VALENTINE (Mixed, mesic Typic Ustipsamment): Psamments are Entisols in poorly graded sands of shifting or stabilized sand dunes. Their age is recent to Pliocene, or older. These soils have a low water-holding capacity and when dry and bare, they are subject to blowing and drifting. Ustipsamments are Psamments with an ustic moisture regime (i.e., moisture usually present only during the growing season). Soils are freely drained sands with mostly grass or savanna vegetation.

The Valentine series occurs above Els, Loup, and Tryon series in the landscape. The soil is deep and excessively drained, with 0-6% slope. The series formed in aeolian sands. The surface soil is dark greyish-brown loamy fine sand 38 cm thick. The subsoil is 64 cm of pale brown fine sand over clay and shaley clay. Runoff is slow due to rapid infiltration and permeability is rapid. Water holding capacity is low. Mean annual precipitation ranges from 41-64 cm, and mean annual temperature is 8-15° C. Soils are dominated by native grass and are used for grazing and haying. Some areas have been cultivated, but readily return to grass unless irrigated. The soil has a northcentral Nebraska, South Dakota, and Kansas distribution.

WILDHORSE (Sandy, mixed, mesic Typic Haplaquept): Aquepts are wet Inceptisols with poor or very poor drainage. The groundwater table usually is close to the surface at some time during the year; depths to water table range from 46 cm in wet years to 107 cm in dry years. Most are Wisconsinan or younger deposits in depressions, very flat plains, or floodplains. Haplaquepts are light colored Aquepts that are found primarily in humid climates. They lack a fragipan but may have groundwater at or near the surface at some time during the year regardless. These soils form primarily in late Pleistocene or Holocene sediments.

The Wildhorse series occurs below Tryon, at the same level as Els, and below Ipage and Valentine series in the landscape. The soil is somewhat poorly drained, and has a 0-3% slope. The soil formed in aeolian sand and sandy alluvium in enclosed Sandhill valleys on stream terraces. The surface soil is composed of strongly alkaline, light greyish-brown to greyish-brown sand 25 cm thick. The subsoil is strongly alkaline, light brownish-grey to grey sand 127 cm thick. Runoff is slow and permeability is rapid. Mean annual precipitation is 41 cm, and mean annual temperature is approximately 8° C. Soils are dominated by native grasses, in particular alkaline species. Land use is primarily for hayland and rangeland. The soil has a western Nebraska distribution.

APPENDIX B

Duncan's multiple range tests for differences among prevalence indices calculated for soil series of Sandhill lakes in 1988; means in the same letter group are not significantly different; Soil Conservation Service hydric soils are denoted by *

Soil	N	Mean	Group
TOTAL FOR ALL LAKES ($F_{8,648}$ = 209.27, Prob > F = 0.0001)			
Valentine	69	3.99	A
Wildhorse	34	3.86	A
Ipage	71	3.82	A
Els	129	3.30	B
Dailey	12	2.91	C
*Tryon	173	2.40	D
*Loup	13	2.47	D
*Hoffland	26	2.41	D
*Marlake	122	1.39	E
BLUE LAKE ($F_{5,49}$ = 30.89, Prob > F = 0.0001)			
Ipage	6	4.08	A
Valentine	17	3.94	A
Els	6	2.34	B
*Tryon	15	2.32	B
*Hoffland	2	1.63	B, C
*Marlake	4	1.21	C
CHRIST LAKE ($F_{4,49}$ = 55.34, Prob > F = 0.0001)			
Valentine	4	3.86	A
Ipage	12	3.41	B
Els	11	3.20	B
*Tryon	13	1.98	C
*Marlake	10	1.17	D
CRANE LAKE ($F_{4,49}$ = 37.49, Prob > F = 0.0001)			
Valentine	5	3.74	A
Ipage	8	3.39	A, B
Els	13	2.98	B
*Tryon	17	2.22	C
*Marlake	7	1.20	D

Soil	N	Mean	Group
CRESCENT LAKE ($F_{4,49}$ = 15.26, Prob > F = 0.0001)			
Valentine	22	4.18	A
Els	10	3.35	A, B
Hoffland	1	3.00	B
*Tryon	7	2.47	B
*Marlake	10	2.26	B
GIMLET LAKE ($F_{4,49}$ = 26.06, Prob > F = 0.0001)			
Valentine	5	4.06	A
Els	16	3.86	A
Dailey	12	2.91	B
*Loup	9	2.45	B
*Marlake	8	1.42	C
GOOSE LAKE ($F_{5,49}$ = 20.30, Prob > F = 0.0001)			
Valentine	6	3.72	A
Ipage	7	3.62	A
Els	10	2.91	B
*Tryon	9	2.59	B
*Loup	4	2.51	B
*Marlake	14	1.58	C
HACKBERRY LAKE ($F_{5,49}$ = 29.78, Prob > F = 0.0001)			
Ipage	9	3.64	A
Valentine	1	3.60	A
Els	16	3.13	A, B
*Tryon	14	2.52	B, C
*Hoffland	1	2.25	C
*Marlake	9	1.32	D
HESSEY LAKE ($F_{5,49}$ = 25.20, Prob > F = 0.0001)			
Valentine	1	3.88	A
Els	10	3.59	A
Wildhorse	14	3.51	A
*Hoffland	5	2.44	B
*Tryon	10	2.35	B
*Marlake	10	1.27	C

Soil	N	Mean	Group
ISLAND LAKE ($F_{3,49}$ = 68.24, Prob > F = 0.0001)			
Ipage	8	4.35	A
Els	8	3.31	B
*Tryon	22	2.18	C
*Marlake	12	1.28	D
MAVERICK LAKE ($F_{4,49}$ = 58.11, Prob > F = 0.0001)			
Ipage	6	4.50	A
Els	11	3.97	A
*Tryon	22	2.58	B
*Hoffland	2	1.59	C
*Marlake	9	1.24	C
MILLER LAKE ($F_{3,49}$ = 119.54, Prob > F = 0.0001)			
Ipage	7	4.52	A
Wildhorse	15	4.31	A
*Tryon	18	2.67	B
*Marlake	10	1.16	C
ROUNDUP LAKE ($F_{4,49}$ = 24.72, Prob > F = 0.0001)			
Valentine	2	4.11	A
Ipage	8	3.43	B
Els	15	3.04	B, C
*Tryon	15	2.41	C
*Marlake	10	1.27	D
WOLF LAKE ($F_{5,49}$ = 29.01, Prob > F = 0.0001)			
Valentine	6	3.95	A
Els	3	3.84	A
Wildhorse	5	3.47	A
*Tryon	11	2.67	B
*Hoffland	15	2.58	B
*Marlake	9	1.52	C

APPENDIX C

Vegetation zones assigned to well sites around Roundup and Island lakes; Soil Conservation Service (1985) hydric soils are denoted by *

Well	USGS No.[a]	Lake	Shore	Soil Series	Vegetation Zone
RO-N1	50	Roundup	North	*Marlake	Emergent
RO-N2	49	Roundup	North	*Tryon	Wet Meadow
RO-S1	48	Roundup	South	*Marlake	Emergent
RO-S2	47	Roundup	South	*Tryon	Wet Meadow
RO-S3	21	Roundup	South	Els	Upland
IS-NW1	53	Island	Northwest	*Marlake	Emergent
IS-NW2	54	Island	Northwest	*Tryon	Wet Meadow
IS-NW3	55	Island	Northwest	*Hoffland	Wet Meadow
IS-NW4	56	Island	Northwest	Els	Upland
IS-NE1	57	Island	Northeast	*Marlake	Emergent
IS-NE2	58	Island	Northeast	*Tryon	Wet Meadow
IS-NE3	59	Island	Northeast	Els	Upland
IS-NE4	60	Island	Northeast	Ipage	Upland
IS-SW1	45	Island	Southwest	*Marlake	Emergent
IS-SW2	46	Island	Southwest	*Tryon	Wet Meadow
IS-SW3	52	Island	Southwest	*Tryon	Upland
IS-SE1	44	Island	Southeast	*Marlake	Emergent
IS-SE2	43	Island	Southeast	*Tryon	Wet Meadow
IS-SE3	51	Island	Southeast	Els	Upland

[a] Well numbers originally assigned by the U.S. Geological Survey.

APPENDIX D

Means of 1989 environmental parameters for individual groundwater well sites

Well	USGS No.[a]	Depth to Water Table (cm)	Specific Conductance (μS/cm)	pH	Soil Moisture Content (%)
RO-N1	50	57	290	6.25	34.9
RO-N2	49	63	113	6.62	20.4
RO-S1	48	27	2658	7.29	24.4
RO-S2	47	77	5769	8.40	5.6
RO-S3	21	194	3385	7.51	2.5
IS-NW1	53	18	264	7.12	50.6
IS-NW2	54	41	384	7.13	21.3
IS-NW3	55	69	672	7.19	17.9
IS-NW4	56	127	525	6.84	2.4
IS-NE1	57	72	552	7.09	28.5
IS-NE2	58	60	587	7.02	20.5
IS-NE3	59	70	405	7.59	17.6
IS-NE4	60	173	131	6.88	1.3
IS-SW1	45	65	563	7.35	16.7
IS-SW2	46	85	516	7.15	9.2
IS-SW3	52	107	485	7.20	3.3
IS-SE1	44	38	745	7.00	22.7
IS-SE2	43	85	458	6.89	6.6
IS-SE3	51	126	517	6.64	1.7

[a] Well numbers originally assigned by the U.S. Geological Survey.

APPENDIX E

General Linear Models procedure for analysis of variance for effect of quadrat location on prevalence indices in 1989

Dependent variable: Prevalence Index

Source	df	SS	Mean Square	F Value	Pr > F
Model	159	41.74	1.99	41.58	0.0001
Error	372	2.58	0.05		
Corrected	531	44.32			

Source	df	Type I SS	Mean Square	F Value	Pr > F
WELL	132	41.53	2.31	48.26	0.0001
QUADRAT	27	0.21	0.07	1.45	0.2382

Source	df	Type III	Mean Square	F Value	Pr > F
WELL	132	41.53	2.31	48.26	0.0001
QUADRAT	27	0.21	0.07	1.45	0.2382

APPENDIX F

Duncan's multiple range test for differences among prevalence indices calculated for quadrats of individual groundwater wells in 1989; means in the same letter group are not significantly different; Soil Conservation Service (1985) hydric soils are denoted by *

Well	USGS No.	Soil	N	Mean	Group
IS-NE4	60	Ipage	28	3.50	A
IS-SE3	51	Els	28	3.24	A
IS-SW3	52	*Tryon	28	2.86	B
IS-NE3	59	Els	28	2.70	B, C
IS-NW4	56	Els	28	2.58	B, C
IS-SE2	43	*Tryon	28	2.53	C
RO-S3	21	Els	28	2.36	C, D
RO-S2	47	*Tryon	28	2.19	D
RO-N2	49	*Tryon	28	1.82	E
IS-NW3	55	*Hoffland	28	1.80	E
IS-SW2	46	*Tryon	28	1.65	E, F
IS-NE2	58	*Tryon	28	1.61	E, F
IS-SW1	45	*Marlake	28	1.46	F, G
IS-NW2	54	*Tryon	28	1.44	F, G
IS-NE1	57	*Marlake	28	1.42	F, G
RO-N1	50	*Marlake	28	1.22	G, H
RO-S1	48	*Marlake	28	1.10	H
IS-NW1	53	*Marlake	28	1.08	H
IS-SE1	44	*Marlake	28	1.00	H

P A R T II

VEGETATION COMPOSITION AND GROUNDWATER IN THE SANDHILLS OF NEBRASKA

VEGETATION COMPOSITION AND GROUNDWATER IN THE SANDHILLS OF NEBRASKA

Nanette E. R. Erickson and Arnold G. van der Valk, Department of Botany, 353 Bessey Hall, Iowa State University, Ames, Iowa 50011 USA

ABSTRACT. Field investigations and laboratory experiments were used to determine the effect of groundwater chemistry on the composition of wetland vegetation and several life-history stages (i.e., seeds, seedlings, and adult plants) of selected wetland species. In 1988, we examined patterns in vegetation composition along north and south shores of 16 lakes in the western Sandhills. North and south shores in these lakes differed in groundwater chemistry. Several species were found primarily along either north or south shores. Vegetation data in 1989 was collected from two lakes with connected groundwater flow. In these lakes, only *Distichlis spicata* had a distribution that was correlated with groundwater chemistry (i.e., pH and specific conductance).

A reciprocal transplant experiment showed that water chemistry had little effect on survival of adult plants. Seed germination experiments conducted using treatments with different water chemistries showed that only *Distichlis spicata* and *Scirpus americanus* seeds could germinate in water

with the highest specific conductance (14,800 μS/cm). Both the seed germination and seedling growth experiments indicated that all water treatments with low levels of dissolved salts (i.e., less than 1,600 μS/cm) had no effect on either seed germination or seedling growth. In a seed bank experiment using two water chemistry treatments, recruitment of Typha spp. was low in seed flats with high specific conductance (7,490 μS/cm), whereas recruitment of Scirpus acutus was unaffected by water chemistry.

Both field observations and experiments support the idea that some differences observed in vegetation composition of wetlands in lakes of the Nebraska Sandhills could be due to differences in groundwater chemistry along north and south shores. Some species seem to be able to become established along south shores because their seeds can germinate when exposed to water with very high specific conductance. However, the composition of the north shore does not appear to result from lack of recruitment of salt-tolerant species. Rather, some other unknown factor affects what species can establish along the north shores.

key words: wetlands, vegetation composition, groundwater hydrology, salt tolerance, Nebraska Sandhills

INTRODUCTION

Vegetation Patterns in Wetlands

Plants along environmental gradients occupy discrete zones when: 1) species are restricted physiologically to some portion of the gradient; 2) species perform better along different portions of the gradient; or 3) all species prefer the same position along the gradient, but are displaced because of interspecific competition, herbivory (Snow and Vince 1984), or other factors such as seed dispersal patterns. Both biotic and abiotic factors have been proposed to explain vegetation patterns in wetland systems. Vegetation zonation have been linked to preemption (Grace 1987), seed dispersal (Parker and Leck 1985), interspecific competition (Snow and Vince 1984, Wilson and Keddy 1986), and herbivory (Lubchenco 1980). Disturbance via wrack burial (Bertness and Ellison 1987), wave action (Keddy 1983), sedimentation (Semeniuk 1980, Catling et al. 1985, Nilsson 1987), water nutrient load (Glaser et al. 1981, Johnson et al. 1987, Wilson and Keddy 1986), and chemical gradients in sediments (Rozema et al. 1983, Ingold and Havill 1984) also may influence macrophyte distribution and zonation. Both biotic and abiotic factors may affect species distributions simultaneously; for example, interspecific competition combined with salt tolerance (Ungar et al. 1979, Bertness and Ellison 1987).

Hydrology and elevation jointly have been correlated with species distributions. Local topography and hydrology were credited with development of bog and fen vegetation patterns in northern Minnesota (Glaser et al. 1981, Glaser 1983) and Labrador (Foster and King 1984). Zonation in tidal wetlands likewise has been attributed to changes in elevation, duration of flooding, and subsequent changes in salinity (Vince and Snow 1984, Armstrong et al. 1985, Ewing and Kershaw 1985).

Groundwater and Vegetation Composition

Gradients in groundwater depth and chemistry affected vegetation patterns in fen meadows of the Netherlands (Grootjans et al. 1985, Bakker et al. 1987). However, the role of groundwater hydrology on vegetation patterns is not easily distinguishable from that of topography. Groundwater movements are moderated by both local and landscape scales of topography. High topographic relief usually is associated with the formation of local groundwater flow systems, whereas low relief results in the formation of regional flow systems (Toth 1963).

Possible correlations between groundwater and plant distributions are confounded by factors other than topography. Porosity of soils influences groundwater movements (e.g., groundwater primarily moves horizontally through porous materials such as gravel and sandstones [Meyboom 1966]) that potentially could create moisture or chemical gradients. Accumulation of salts and carbonates in the soil profile often results from groundwater fluctuations (Miller et al. 1985, Mills and Zwarich 1986). Gradients in dissolved oxygen, specific conductance, and pH have developed as a result of groundwater fluctuations (Ransom and Smeck 1986). Vegetation zonation has been attributed to soil moisture gradients caused by a fluctuating groundwater table (Seischab 1983). Resulting nutrient gradients caused by groundwater movements affected the distribution of Nuphar advena in two Michigan bogs (Keough and Pippen 1983).

Wetland Vegetation of the Nebraska Sandhills

The Sandhills of Nebraska, the largest continuous dune complex in the western hemisphere, covers an area of approximately 52,000 km^2 (Keech and Bentall 1978) (Figure 1). This region is one of the most extensive tracts of the North American native grassland biome (Barnes and Harrison 1982). Vegetation of the Sandhills is a mosaic of prairie and wetlands, with pockets of pine and deciduous forest; an estimated 557,590 ha of wetlands are contained within the Sandhills (Rundquist et al. 1981).

Vegetation zonation is evident in wetlands of the Sandhills of Nebraska. Indeed, at the beginning of the 20th century, Pool (1914:291) documented the presence of vegetation bands in conjunction with Sandhill lakes and ponds. Present-day observations suggest that vegetation patterns in the Nebraska Sandhills closely follow the topography of the dunes, which in turn may correspond to the groundwater table configuration (see Lissey 1971).

Groundwater flow and groundwater chemistry of the western Sandhills are related. Lakes along an elevational gradient become less alkaline as elevation decreases (Winter 1989). A conductivity gradient also develops within individual lakes because water is lost via evaporation; groundwater discharge sites along north shores are relatively fresh compared to recharge sites along south shores (Winter, personal communication). Groundwater hydrology of the Nebraska Sandhills may partially explain some unusual vegetation patterns found in some Sandhill wetlands. Sandhill lakes often have freshwater wetland species growing along north shores and alkaline species growing along south shores.

Our study examined this relationship between wetland vegetation and groundwater in the Nebraska Sandhills. We tested the hypothesis that differences in the composition of vegetation along north and south lake shores is due to differences in groundwater chemistry. Three different approaches were used. First, a vegetation survey was conducted along the north and south shores of 16 Sandhill lakes in 1988. Second, vegetation and environmental conditions were examined in more detail from permanent quadrats along two lakes, over the 1989 growing season. Finally, a series of field and laboratory studies examined the effect of different water chemistries on seed germination, seedling growth, and adult survival.

STUDY AREA

> Spring came to the range country with the swiftness of the swallows. In the morning snowdrifts lay deep along the wagon trails. In the evening the low valleys gleamed with lakes of rose and orange reflecting the delicate sky. In a few days translucent grasses pushed through the shallower reaches, misting the blue with green. Wild ducks darkened the open water and quacked and quarreled as they fed along the shores. In the swamps the hell-divers chattered and mud hens fought or led their early hatchings out for swims, a dozen wine-colored plush birdlings bobbing along behind the black hen mother.[1]

Vegetation of the Sandhills

Vegetation of the Sandhills grows in a semiarid climate, in which a moisture deficit exists for much of the growing season (Wilhite and Hubbard 1990).[2] Temperature and precipitation exhibit similar patterns across the Sandhills, with higher values in the eastern region that diminish toward the west. Mean annual precipitation ranges from 63.5 cm in the east to 37.6 cm in the west (Rundquist 1983), whereas mean annual temperature ranges from 9.4^{o} C in the east to 8.9^{o} C in the west (Wilhite and Hubbard 1990). Annual temperatures range from -40.0^{o} C in January to 43.3^{o} C in July (Rundquist 1983). Approximately 80% of the precipitation falls between April and September; however, nearly 75% of all annual

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[1] "The Hills," an excerpt from Old Jules (Sandoz 1935:348)

[2] An extensive description of Sandhill vegetation is found in part I, "Utility of the 'unified federal method' for delineating wetlands in the Nebraska Sandhills;" portions have been repeated as reference

precipitation is lost via evaporation or transpiration (Rundquist 1983). Climate limitations have rendered land use primarily to rangeland, although row cropping is possible with center pivot irrigation.

Most native vegetation of the Sandhills is in either prairie or wetland habitat, with occasional forests. Although plant species are similar to those found throughout the northern prairie, the combination of species in the Sandhills is unique (Kaul 1990). The Sandhills were explored botanically starting in the late 19th century; flora of the central Sandhills region initially was documented by Webber (1889), whereas the western Sandhills were surveyed by Rydberg (1895).

Pool (1914) is credited with the first ecological study of the Sandhills. He classified vegetation as either "upland" or "lowland" formations, and also distinguished between alkaline and freshwater ponds and lakes. Pool (1914:291) provided the first documentation of wetland zonation in the Sandhills, citing the "highly developed... belt or a series of belts about lakes and ponds and in the lower valleys in many parts of the Sandhills." Pool (1914:307) stated that soil moisture and alkalinity gradients affected wetland species distribution; for example, decreasing soil moisture and receding water table altered vegetation composition.

Soils of the Sandhills

From 37 million years to present, both alluvial and aeolian forces shaped the Sandhills (Swinehart and Diffendal 1990).[3] Alluvial sediments were deposited during the Pliocene (ca 1.6-5.0 million years before present) by a precursor of the North Platte River, and accumulated for at least one million years. Dune formations are believed to have occurred no earlier than 10,000 years before present; dune orientation began an estimated 7,000 years ago as a result of prevailing northwest winds (Swinehart 1984). Dunes of the Sandhills are stabilized by the vegetation cover that is supported by rainfall. Swinehart (1990:51) predicted that reducing vegetation to 20% cover would create large-scale dunes and an active "sand sea."

Most soils of the Sandhills are highly erodible, and soil "blowouts" occur readily if vegetation cover is insufficient or disturbed; Rydberg (1895) documented blowouts 100 m in diameter and 15 to 20 m deep. The soils encountered at our study area were predominantly Mollisols and Entisols. Mollisols are prairie soils that have a prominent mollic epipedon. Certain Mollisols develop in low places where water collects and stands, but some are on broad flats or seepy

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[3] An extensive description of soils is found in part I, "Utility of the 'unified federal method' for delineating wetlands in the Nebraska Sandhills;" portions have been repeated as reference

hillsides (Soil Conservation Service 1975). Vegetation usually consists of grasses, sedges, and forbs. The Entisols are soils of recent to Pliocene age that are characterized by A and C Horizons but no B Horizon. Psamments dominate the Sandhills; these Entisols are characterized by well sorted sands of shifting or stabilized sand dunes (Soil Conservation Service 1975). Psamments have a low water-holding capacity; when dry and bare, they are subject to blowing and drifting. Vegetation typically is grass or savanna (Soil Conservation Service 1975).

Groundwater in the Sandhills

An estimated 8.6×10^{11} to 9.9×10^{11} m^3 (7.0×10^8 to 8.0×10^8 ac-ft) of groundwater is in storage underneath the Nebraska Sandhills (Reed 1966 as cited by Keech and Bentall 1978). The groundwater is held within a portion of the "High Plains Aquifer," commonly known as the "Ogallala Aquifer;" the largest part of this formation is contained beneath the Sandhills. In general, groundwater in the Sandhills moves in an east-southeast direction across Nebraska (Dreeszen 1984). Depth to water table varies from as much as 100 m at the top of dunes to near or at the surface (Bleed 1990).

Much of the Nebraska Sandhills is a closed drainage area in which precipitation is the primary source for groundwater recharge. Groundwater in the Sandhills is "soft," containing relatively low levels of bicarbonate and calcium compared to the rest of the State; minerals are dissolved slowly because precipitation is only slightly acidic (Bleed 1990). Groundwater contamination was not an issue when the Sandhills were used only as open rangeland; however, increased agriculture and feedlots in the area pose new threats. Potential contaminants have very little time to be removed by chemical or biological processes before reaching the aquifer because of rapid infiltration through the sandy soils and sparse vegetation mat (Bleed 1990).

Groundwater movements in the Nebraska Sandhills can be conceived of along landscape, regional, and local scales. Although groundwater flows easterly through much of the State, the direction of groundwater flow in the western Sandhills landscape is determined by a "groundwater high" in Sheridan and Garden counties. This high apparently resulted from uplift along the Chadron Arch; to the east of the high, groundwater flows to the east, and conversely groundwater moves west on the western side of the groundwater high (Novacek 1989).

On a regional scale, groundwater moves along elevational gradients, with seepage from higher toward lower lakes (Winter 1989). Chemical differences have been associated with this groundwater seepage; lakes at high elevations have registered a specific conductance of 10,000 $\mu S/cm$ compared to less than

1,000 μS/cm for lower lakes (Winter, personal communication as cited by LaBaugh 1986). Groundwater discharge occurs where the water table slopes into a lake, whereas recharge occurs as the water table slopes away from the lake (Winter 1989).

Within individual lake basins, water chemistry gradients arise in conjuction with local groundwater patterns. Typically, groundwater discharge occurs at the north and recharge at the south shore of a lake; the north shore typically is at a higher elevation than the south shore, which results in groundwater flowing south. In systems other than the Sandhills, groundwater recharge sites typically contain low levels of carbonates and salts compared to discharge areas (Miller et al. 1985). In the Sandhills, however, surface water in the semiarid climate is lost via evaporation, and so the groundwater becomes more concentrated as it moves south within the lake. Hence, a conductivity gradient develops in which water associated with south shores has a greater concentration of dissolved salts, and therefore higher specific conductance, than that of water associated with the north shores (Winter, personal communication). Groundwater recharge from Sandhill lakes initially increases concentrations of dissolved salts in the groundwater. However, recharge at topographic depressions between lakes (Winter 1986) results in an overall decrease in groundwater salt concentrations from higher to lower elevation lakes.

Winter (personal communication) hypothesized that groundwater gradients should be more pronounced in the northern, higher elevation lakes because they receive fewer inputs of freshwater along the north shores compared to the southern lakes. The southern lakes typically have larger watersheds that experience more surface runoff to the north shores, and consequently dilute any chemical gradients potentially within the groundwater.

Wetlands and Lakes of the Sandhills

Sandhill wetlands may be associated with lakes or exist as wet meadows in topographic depressions. Wetlands and lakes of the Sandhills may be maintained through either rainfall or groundwater (Bleed and Ginsberg 1990); however, most wetlands in the Sandhills are sites of groundwater discharge (Ginsberg 1984). Groundwater depletion via center-pivot irrigation is considered the primary cause of wetland habitat destruction in the Sandhills. By 1986, wetland losses were estimated in excess of 30% for the entire Sandhills region, with losses over 90% in Loup County in the eastern Sandhills (Gersib, personal communication).

An estimated 1,500 to 2,500 permanent and ephemeral lakes are located in the Sandhills (Novacek 1989). Lakes throughout the Sandhills are generally small, although some are 1.6 km wide and 4.8 km long (Bleed and Ginsberg 1990). Most lakes of the Sandhills are shallow, with mean depths of 0.8 to 1.2 m; Blue Lake within Crescent Lake National Wildlife Refuge is the deepest (4.3 m) (McCarraher 1977). Lakes of the Sandhills can be classified as: 1) groundwater lakes; 2) lakes in poor connection with groundwater; and 3) perched lakes with no groundwater connection (Ginsberg 1984). Alkalinities of Sandhill lakes range from near zero to more than 90,000 mg/l, one of the highest measurements recorded for natural lakes (Schnagl 1980, as cited by Bleed and Ginsberg 1990). In general, though, lakes become fresher moving east to southeast across Nebraska (Dreeszen 1984). The "closed-basins area" in the western Sandhills ordinarily lacks surface outflow except during very wet periods (Keech and Bentall 1978). Most lakes and wetlands in the closed-basins area are maintained by surface runoff rather than groundwater, and are characteristically alkaline. Approximately 98% of the highly alkaline lakes in the Sandhills occur in the closed-basins area (Bleed and Ginsberg 1990).

Study Site

Our study site was located in Garden County, Nebraska, one of the western-most counties in the Sandhills (Figure 1). Data were collected from lakes within and around Crescent Lake National Wildlife Refuge. This 18,630 ha refuge was established in 1938 primarily for the purpose of waterfowl management. Crescent Lake National Wildlife Refuge normally receives 41.9 cm annual precipitation; above average annual precipitation was recorded in 1988 (47.8 cm). In 1988, vegetation was inventoried from 16 lakes: Goose, Gimlet, Roundup, Shafer, Hackberry, Island, Christ, Deer, Crane, and Blue lakes within the refuge boundaries, Crescent Lake south of the refuge, and Miller, Maverick, Wolf, Brewer, and Hessey to the north (Figure 2).

From June through August 1989, vegetation was sampled weekly in association with 19 groundwater wells around Roundup and Island Lakes of Crescent Lake National Wildlife Refuge (Figure 3). Well lines were established perpendicular to the shores of Roundup and Island lakes. These two lakes are connected by groundwater flow, with the detected outflow from the south end of Roundup Lake entering along the north shore of Island Lake (Winter 1986). Groundwater of these two lakes is dominated by bicarbonate, the most common anion, and either calcium or sodium, the most abundant cations (LaBaugh 1986). Roundup Lake had two wells on the north shore and three wells on the south. Island Lake had two parallel well lines on the north shore, each with four wells, and two lines on the south shore, with three wells apiece.

METHODS

Groundwater Well Installation

With the assistance of Dr. Tom Winter of the U.S. Geological Survey, 18 groundwater wells were installed in August 1988 and June 1989. Four groundwater wells were positioned at Roundup Lake; one preexisting well also was incorporated into the sampling scheme. The north well line had two wells and the south three wells. Fourteen wells were placed around Island Lake. Two parallel well lines were located on the north shore, each with four wells. Two lines also were established on the south shore, each with three wells. Numbers originally were assigned to the wells by the U.S. Geological Survey. We assigned a three to four letter code to represent the lake and shore position (e.g., RO-S for Roundup Lake, south shore) and a number to indicate the position in the well line. Wells assigned the smallest number were sites with emergent vegetation, whereas wells with the largest number were sites with upland vegetation; intermediate well numbers indicated sites with mixed vegetation.

Each well was constructed from a 61.0-cm-long (2.0 ft) PVC screen (10-slot, 0.03 cm [0.01 in] mesh) glued with PVC cement onto a PVC pipe of 5.1 cm (2.0 in) diameter. Well length was based on the estimated depth to groundwater at a site. Holes were hand-augered to a depth approximately 1 m below the water table, and the well was inserted. The hole around the well was filled with bentonite to prevent downward water movement.

Water Chemistry and Depth Measurements

Wells were monitored on a weekly to bimonthly basis from June through August 1989. Depth to the groundwater table from the soil surface was determine by using a 30.1 m (100.0 ft) metal tape weighted with lead sinkers. Depth measurements were recorded to the nearest 2.5 cm (1 in); depth of surface water was not incorporated into these measurements. Water samples from the wells were collected using a Nalgene hand-operated vacuum pump. Specific conductance was measured in the field with a Hanna HI 8333 conductivity meter; samples were stirred gently when measured. Water samples then were taken to the field laboratory and analyzed for pH using an Orion portable pH meter (model SA 250). A Ross pH electrode was used in conjunction with an automatic temperature compensation probe. Prior to sampling, the probe was calibrated manually using buffers of pH 7 and 10. Samples were stirred gently while pH was determined. Weekly measurements were discontinued on 15 August 1989.

Soil Moisture Content

Soil cores were collected weekly to bimonthly from June to August 1989. Cores of approximately 3.8 cm (1.5 in) diameter and 20.3 cm (8.0 in) length were taken with a soil probe. Soils were collected from the four permanent vegetation quadrats at each well site, placed into preweighed soil tins, and returned to the field laboratory. Cores were weighed wet, then placed in a drying oven (ca 80^{o} C) for 8-10 hours. Soil cores were reweighed, and percent water content was calculated for each sample. Weekly measurements were discontinued on 15 August 1989.

Vegetation Composition and Environmental Parameters

In 1988, we surveyed vegetation along north and south shores of 16 lakes that were oriented along a general north to southeast line. Five transects were positioned at the north and south shores of the lakes. Each transect began in emergent habitat and ended in the upland prairie vegetation. Five quadrats (0.5 m^2) were sampled along each transect at approximately equal intervals; percent cover for each plant species was estimated in each quadrat. Samples of all unknown species were collected for later verification at the Ada Hayden Herbarium, Iowa State University, Ames; all nomenclature followed the Great Plains Flora Association (1986).

During the 1989 field season, four permanent vegetation quadrats (0.5 m^2) were placed at each groundwater well at Roundup and Island lakes (see Figure 3). Quadrats were spaced at 1 m intervals along a line parallel to the lake shore, with the well at the center of the line. Percent cover was estimated for each species; quadrats were examined weekly to bimonthly for species composition. Cover estimates were discontinued on 15 August 1989.

Two approaches were employed to detect trends in species distribution that could correspond to known groundwater patterns in the Sandhills. First, we calculated cumulative covers for species by north and south shores of lakes sampled in 1988 and 1989. Cumulative cover was sum of percent cover by species measured within quadrats per shore per lake. In 1988, cumulative cover was calculated from 50 quadrats; all species comprising less than 40% of total vegetation cover were eliminated from further analysis. In 1989, the number of quadrats varied among shores, depending on the number of well sites (with four quadrats per site); all species comprising less than 5% of total vegetation cover were eliminated from further analysis. A species was considered to favor either north or south shores if its cumulative cover for one shore comprised more than 75% of the total vegetation cover. We then assumed that the species distribution was not random but skewed instead.

Secondly, we calculated means of environmental measurements made in 1989 at individual wells, and compared these to percent cover means calculated for 17 dominant species. We performed correlation analyses to indicate relationships among environmental measurements and dominant vegetation; data were analyzed using SAS on the Iowa State University mainframe computer. Pearson correlation coefficients were calculated for the 17 species and water table depth, specific conductance, pH, and soil moisture content.

Reciprocal Transplant Experiment

We tested the effects of groundwater chemistry on mature plants with a reciprocal transplant experiment initiated in June 1989. Roundup Lake was chosen for the study site because its north and south shores have distinctly different water chemistries and vegetation. Dominant species of the north and south shores of the lake were selected for the experiment; transplants were made with each of four species: *Scirpus americanus*, *Scirpus fluviatilis*, *Distichlis spicata*, and *Spartina pectinata*. *Scirpus americanus* and *Distichlis spicata* were dominant species along the south shore, whereas *Scirpus fluviatilis* and *Spartina pectinata* were dominant on the north shore.

Individual plants were collected beginning on 14 June 1989, and planted on 16 June 1989. Species were transplanted into habitats identical to those from which they came; i.e., the two emergent species (*Scirpus americanus* and *Scirpus* fluviatilis) were transplanted to emergent habitats, whereas the wet meadow species (Distichlis spicata and Spartina pectinata) were transplanted into wet meadow habitats. For each species, 10 plants were transplanted in place: five into buckets with drainage holes and five directly into the ground at their source. Ten plants also were transported to the opposite shore; five were planted directly into the ground and five were planted in buckets. Because potted plants seemed to be root bound, they were removed from buckets on 11 August 1989. Weekly observations on the transplantings were discontinued on 13 August 1989; follow-up observations of the plantings were made on 23 September 1989 and 23 May 1990. Chi-square goodness-of-fit tests were performed on the data; chi-square was calculated for each species using the observed survival and an expected survival of 10 transplants per shore.

Seed Germination Experiment

Seed heads from Distichlis spicata, Scirpus americanus, Scirpus maritimus, Carex scoparia, Carex vulpinoidea, and Carex praegracilis were collected from July to August 1989 at Crescent Lake National Wildlife Refuge (Appendix A). Seed heads were stored in a cold room (ca 4^{o} C). Seeds were removed from their inflorescences beginning 22 January 1990. A #10 soil sieve was used to separate larger materials from the seeds, then an air column separated the seeds from the remaining chaff (Appendix B).

Water samples were collected between 23 and 24 May 1990 from 10 locations from Crescent Lake National Wildlife Refuge. The 10 locations were representative of north and south shores of four lakes (i.e., Island, Hackberry, Roundup, and Goose) plus water from an artesian well and perched wetland depression near Roundup Lake (Appendix C). These water samples were stored in a cold room (ca 4^{o} C).

Germination experiments were conducted at the Seed Laboratory at Iowa State University from May through September 1990. Each experiment for a given species consisted of 10 different water treatments, with each treatment replicated three times; treatments were nine waters collected from Crescent Lake National Wildlife Refuge, plus deionized water. Water from the artesian well was not used in this experiment. Each replicate contained 100 seeds placed on two sheets of standard blue blotter paper in a plastic box (22.9 cm x 15.2 cm x 5.1 cm). The blotter papers then were moistened with 60 ml of an appropriate water sample; additional water was added as needed to maintain moist conditions throughout the experiment. Replicates were kept at 20^{o} C for 16 hours in darkness and 30^{o} C for 8 hours in light. Seeds were considered germinated only if both roots and shoots developed normally. Experiments for each of the six species were run as long as seeds continued germinating. Data were analyzed using SAS on the Iowa State University mainframe computer. Analysis of variance procedures for balanced designs were used to test effects of water treatments on seed germination.

Seedling Growth Experiment

Seedlings from two wetland species were grown hydroponically in fine grade silica sand and 10 water chemistry treatments using water collected from Crescent Lake National Wildlife Refuge, including the artesian well. One-hundred sixty plastic pots (8.3 cm x 8.3 cm x 7.6 cm) were lined along the bottom with absorbent cotton, and then filled with sand. Two pots were placed into each of 80 plastic flats (20.3 cm x 10.2 cm x 5.1 cm), with eight flats per water treatment. Approximately 30 seeds of *Scirpus maritimus* were planted in one of the two pots per flat on 2 August 1990; the remaining pots were planted with *Carex scoparia*. Seeds were covered with a thin layer of sand (approximately 0.5 cm). Flats were watered daily or as needed using the appropriate water treatment. Survival of seedlings was monitored through 10 September 1990. Seedlings from each pot then were counted, harvested, and weighed. Data were analyzed using SAS on the Iowa State University mainframe computer. Analysis of variance procedures for balanced designs were used to examine if the water chemistry treatments affected the mass of *Scirpus maritimus* and *Carex scoparia* seedlings.

Seed Bank Experiment

Soil for seed bank analysis was collected on 24 May 1990. Soil was sieved through hardware cloth in the field in order to remove roots and rhizomes, and then transported to the cold room. The soil was homogenized with a cement mixer prior to its use in the seed bank experiment.

Drainage holes were drilled in 60 plastic planting flats (20.3 cm x 20.3 cm x 5.1 cm). Each flat with drainage was nested inside of a second flat with no drainage. Approximately 2.0 cm of greenhouse sand was placed in the bottom of each inside flat, and covered by 2.0 cm of soil from the study site. In addition to the 60 flats, three more nested flats, containing 4.0 cm of greenhouse sand, were incorporated into the study to detect any contamination by seeds from greenhouse plants.

Two watering treatments were used (i.e., recycled and leached), with 30 replicate flats of each treatment. The treatment flats were arranged in a stratified block design. In the recycled treatment, water was recycled daily from the outer flat to the nested inner flat in 30 flats to maintain a high level of dissolved salts in the soil and water. In the leached treatment, tap water (300 μS/cm) was applied daily to another 30 flats in order to gradually leach salts from the soil. "Leached" and "recycled" rows were alternated, with four flats per row. Three seed contamination flats were placed in three different "leached" rows; the contamination flats also received tap water daily.

The seed bank experiment began on 10 July 1990, and the specific conductance of the water in the recycling treatment was measured weekly. The number of seeds of species that germinated from the seed bank were counted weekly, beginning on 17 July 1990. The seed bank study was completed on 14 August 1990. Analysis of variance procedures then were used to determine the effect of watering treatments on recruitment from the seed bank.

RESULTS

Water Chemistry and Depth Measurements

Depth to the groundwater table in all wells generally decreased as the field season progressed (Appendices D and E). Depth to water table varied from 2.5 cm at wells IS-NW1 and IS-SE1 to 200.7 cm at RO-S3. No seasonal fluctuations were observed in specific conductance, although site to site variations occurred. The highest specific conductances (over 3,000 $\mu S/cm$) were observed consistently at RO-S1, RO-S2, and RO-S3, whereas the lowest measurements (100 to 122 $\mu S/cm$) occurred at well RO-N2 (Appendix F). Values of pH ranged from 6.38 to 8.45 (Appendix G). Well RO-S2 had both the highest pH value (8.45; 18 July 1989) and specific conductance (7,780 $\mu S/cm$; 2 July 1989).

Soil Moisture Content

Mean values for percent water content among well sites varied from 0.9% at IS-SE3 and IS-NE4 to 52.4% at IS-NW1 (Appendix H). Mean soil moisture content was greatest for wells located in emergent vegetation and least for wells found in upland vegetation. Moisture content at all sites generally decreased as the field season progressed.

Vegetation Composition and Environmental Parameters

One-hundred fifty-nine species were identified from 650 quadrats from 16 lakes in 1988. Species with skewed distributions (i.e., cumulative cover was more than 75% along only one shore) were observed at all 16 lakes (Appendix I). Crane and Island lakes contained the fewest species with skewed distributions (25.0% and 28.6%, respectively), whereas Crescent Lake contained the most species with skewed distributions (86.7%) (Table 1). *Distichlis spicata* was the only species in 1988 that favored one shore consistently; it was found mostly along the south shores (Table 2). In 1989, all four dominant species at Roundup Lake had preferential shore distributions (Appendix J). *Panicum virgatum* and *Distichlis spicata* were found only along north and south shores, respectively.

Fifty-nine species were identified from 76 quadrats measured weekly at Roundup and Island lakes during the 1989 field season. Correlations among species abundance and environmental data indicated that the abundance of only one species was correlated with any environmental parameters measured. *Distichlis spicata* abundance was positively correlated with both the specific conductance ($r = 0.9014$, prob > $r = 0.0001$) and pH ($r = 0.7139$, prob > $r = 0.0006$) of the groundwater.

Reciprocal Transplant Experiment

Fewer transplants survived on the south shore of Roundup Lake, compared to the north shore, based on observations made on 23 May 1990 (Table 3). Three species had 100% survival on the north shore (i.e., Scirpus fluviatilis, Distichlis spicata, and Spartina pectinata). The loss of the Scirpus americanus transplant on the north shore could not be attributed to water chemistry exclusively, because these transplants showed evidence of white-tailed deer (Odocoileus virginianus) herbivory.

Chi-square goodness-of-fit tests indicated that dominant species from the north (i.e., Spartina pectinata and Scirpus fluviatilis) and south (i.e., Distichlis spicata and Scirpus americanus) shores showed no increased mortality when transplanted along the north shore. However, all species transplants had lower survival rates along the south shore, with the exception of Spartina pectinata.

Seed Germination Experiment

Seeds of most species germinated equally well in the eight water chemistry treatments with dissolved salt concentrations less than 1,600 $\mu S/cm$. Only two species (i.e., Distichlis spicata and Scirpus americanus) had any seeds germinate in water collected from the Roundup depressional wetland (14,800 $\mu S/cm$) (Appendix K).

The analysis of variance procedures indicated that water chemistry treatments affected seed germination of some species (Table 4). Water chemistry treatments had no effect on Distichlis spicata, Scirpus americanus, or Carex praegracilis germinations. Scirpus maritimus, Carex vulpinoidea, and Carex scoparia had relatively few seeds germinating in water from the south shore of Goose Lake (7,000 μS/cm) (29.3%, 28.0%, and 0.0%, respectively), and no seeds germinating in water from the Roundup depressional wetland (14,800 μS/cm) (Appendix K). Some seeds from selected species developed abnormally in various water treatments; these data are given in Appendix L. Another set of analyses was performed where germination data for the Goose Lake south (7,000 μS/cm) and Roundup depressional wetland (14,800 μS/cm) treatments were eliminated. Differential germination was no longer detectable in Scirpus maritimus ($F_{1,6}$ = 0.864, prob > F = 0.3885), Carex vulpinoidea ($F_{1,6}$ = 0.064, prob > F = 0.8090), or Carex scoparia ($F_{1,6}$ = 1.55, prob > F = 0.2590) (Appendix M).

Seedling Growth Experiment

Good germination and seedling growth were observed for Scirpus maritimus and Carex scoparia seedlings in the eight water treatments with dissolved salt concentrations less than 1,600 μS/cm. Roots were stunted in Scirpus maritimus seedlings grown in water from the south shore of Goose Lake

(7,000 μS/cm); no _Carex scoparia_ seedlings grew in this water. Neither species grew in water collected from the Roundup depressional wetland (14,800 μS/cm). Mass of _Scirpus maritimus_ and _Carex scoparia_ seedlings versus specific conductance values for the 10 water treatments are given in Figures 4 and 5, respectively.

An analysis of variance ($F_{1,8}$ = 38.17, prob > F = 0.0003) indicated a significant difference in mean mass of _Scirpus maritimus_ seedlings when grown hydroponically in different water treatments (Table 5). This effect was due primarily to the reduction in growth in treatments using water from Goose south (7,000 μS/cm) and Roundup depressional wetland (14,800 μS/cm); no significant difference ($F_{1,8}$ = 1.469, prob > F = 0.2711) was observed when these two treatments were removed from analysis.

Likewise, analysis of variance ($F_{1,8}$ = 12.21, prob > F = 0.0081) indicated that mean mass of _Carex scoparia_ seedlings differed when grown hydroponically in different water treatments (Table 5). Again, this effect was due primarily to reduced growth in treatments using water from Goose south (7,000 μS/cm) and Roundup depressional wetland (14,800 μS/cm), and no significant difference ($F_{1,8}$ = 8.573, prob > F = 0.0264) was observed when these two treatments were removed from the analysis.

Seed Bank Experiment

Plants that emerged from the seed bank in 1990 were assigned to four groups prior to data analysis. "Scirpus spp." primarily consisted of *Scirpus acutus*, with a few individuals of *Scirpus fluviatilis* and *Scirpus maritimus*. "*Typha* spp." plants most likely were *Typha angustifolia*, rather than *Typha latifolia*, because this was the most common species at the soil collection site. The species of each *Typha* seedling could not be determined because they never flowered. However, species identification was not critical for data analysis because *Typha latifolia* and *Typha angustifolia* exhibit similar tolerances to dissolved salts (Kantrud et al. 1989). All remaining plants were grouped as either "forbs" or "grasses;" these constituted only a minor component of the seed bank.

Results of the analysis of variance indicated that the recycled water treatment had significantly higher specific conductance ($F_{8,15}$ = 234.86, prob > F = 0.0001) than the leached water treatment (Table 6). The water chemistry treatments had no effect on the number of *Scirpus* spp. seeds that germinated and developed ($F_{8,15}$ = 0.03, prob > F = 0.8630). Likewise, germination and growth of grasses ($F_{8,15}$ = 0.86, prob > F = 0.3838) and forbs ($F_{8,15}$ = 4.62, prob > F = 0.0688) were not significantly affected by the treatments. However, the recycled water treatment did significantly reduce the germination and recruitment of _Typha_ spp.; means were 0.21 plants/flat in the recycled treatment and 1.38 plants/flat in the leached treatment ($F_{8,15} = 16.32$, prob > F = 0.0049) (Table 6).

DISCUSSION

Vegetation Composition and Groundwater Chemistry

Our hypothesis that vegetation composition is influenced by differences in water chemistry is not without precedence. In northern Minnesota, Glaser et al. (1981) observed that vegetation patterns in peatlands were closely associated with both the flow and chemistry of surface waters. Species distributions in oxbow lakes of Alberta were correlated with nutrient gradients (Lieffers 1984). Furthermore, Grootjans (1985) documented a relationship between groundwater and vegetation distribution in wet meadows of the Netherlands. He found that most species showed distinct preference or avoidance for different groundwater types, ranging from very low to very high concentrations of dissolved ions. He further concluded that these species were "faithful" to the plant communities associated with different groundwater chemistries.

Our hypothesis that vegetation composition would differ between north and south shores presumed that water chemistry differences indeed existed between the respective groundwater discharge and recharge areas within Sandhill lakes (Winter, personal communication). Before exploring vegetation differences between north and south shores, it seems wise to first address the premise on which our hypothesis is based. Our 1990 water chemistry data illustrate that the specific conductance of water was higher for south shores when compared to north shores of individual lakes (Appendix C). One notable exception was Island Lake, whose groundwater along the northeast and south shores contained similar amounts of dissolved salts. Our findings, however, were consistent with Winter's data (Winter 1986) that portions of the northeast shore of Island Lake, like the south shore, were sites of outflow; hence, a chemical gradient should not form between these shorelines.

Having concluded that groundwater chemistries do differ between north and south shores of most lakes, we then set out to verify whether vegetation composition also differed between shores. In 1988, we found that several species favored either north or south shore consistently, notably Distichlis spicata on south shores at 12 of 13 lakes, Agrostis stolonifera on north shores at seven of 11 lakes, and Polygonum amphibium on north shores at five of 10 lakes. The preferential distributions of these three species were in accord with their known respective tolerances to dissolved salts (see Table 7).

We expected that the north-south pattern would be more pronounced in higher elevation, more alkaline lakes in the north of our study area compared to the less alkaline southern lakes of lower elevations. Although several species displayed skewed distributions, relationships among lake location, elevation, alkalinity, and species distributions were not obvious. Miller Lake (elevation 1183 m) at the northern end of our study area had 53.3% of its dominant species with skewed distributions, whereas Crescent Lake (elevation 1152 m) at the south end had 86.7% of the species with skewed distributions. Goose Lake had both high elevation and alkalinity, but did not display the north-south pattern as much as the low elevation, low alkalinity Crescent Lake (see Table 1). We also examined whether the skewed distribution of Distichlis spicata was more distinct at higher elevation, alkaline lakes (see Table 2). However, this species showed such a strong preference for south shores that no elevation trend could be distinguished. Although certain plant species favor north or south shores of Sandhill lakes, we are unable to detect any trends in vegetation composition associated with lake elevation.

Surprisingly, in 1989, we did not find many correlations between dominant plant species abundance and water chemistry. Only Distichlis spicata correlated with specific conductance and pH. This species was found only at the two well sites (RO-S2 and RO-S3) that had relatively high specific conductance values, but easily within the tolerance range of Distichlis spicata (Table 7).

Adult Mortality and Water Chemistry

In the reciprocal transplant experiment, transplant shock did not cause significant mortality because ample root masses were transferred. Likewise, soil moisture was not an issue because we were transplanting in emergent and wet meadow habitats, both with sufficient water available. The dominant species along the north shore had 100% survival when transplanted along the north shore.

Increased mortality along the south shore could result from differences in water chemistry. We assumed that well data from 1989 were representative of water chemistries experienced by the transplants because the transplants were made close to these wells (see Appendices F and G). Transplants of Distichlis spicata and Scirpus americanus had nearly 100% survival along the north shore of Roundup Lake. When combined, transplants of these two dominant species from the south shore fared less well along the south shore than did north shore species (i.e., Spartina pectinata and Scirpus fluviatilis) transplanted along the north shore (Table 3). South shore species survived better when transplanted along the north shore. This suggests that groundwater chemistry along the south shore is stressful even to plants that normally can tolerate such conditions. Similarly, Bertness and Ellison (1987) found that all reciprocal transplants of salt marsh species performed better in the low stress habitat (i.e., less anaerobic), regardless of their source habitat.

All four species had fewer transplants survive along the south shore than along the north shore. In all instances, though, these species were exposed to dissolved salt concentrations that were within their known tolerance levels (see Table 7). Even _Scirpus_ _fluviatilis_, with the lowest survival of 60%, would have encountered maximum salt concentrations of only 3,000 μS/cm (well RO-S1, Appendix F), easily within its reported tolerance (Table 7). Similarly, nine _Spartina_ _pectinata_ survived at the south shore, compared to eight indigenous _Distichlis_ _spicata_ transplants, despite the latter being more tolerant of dissolved salts than the former (Table 7). This effect of water chemistries on the survival of adult plants along the south shore is not sufficient to explain the north-south distributions of species, however.

Although some transplant mortality occurred at the south shore, most transplants were able to survive despite exposure to water chemistry with high amounts of dissolved salts. In other words, rapid or drastic changes in water chemistry that can occur along some portions of Sandhill lake shores (Winter 1986) should have little effect on the survival of adult plants. In fact, species indicative of freshwater and alkaline habitats often are found growing together. If adult plants are relatively unaffected by differences in the water chemistries between north and south shores, then the north-south distribution patterns in the Sandhills are not a result of differential adult mortality.

Recruitment and Water Chemistry

The seed germination experiment showed that seeds of selected wetland species responded differently to the water chemistry treatments; some species were unaffected by increasing concentrations of dissolved salts, whereas other species were unable to germinate at high salt concentrations. In a comparable study, Galinato and van der Valk (1986) found that seeds of selected wetland species had varying sensitivities to sodium chloride concentrations. For example, germination of Scolochloa festucacea and Typha glauca were reduced in 1,000 mg/l NaCl, whereas 5,000 mg/l NaCl had no effect on Hordeum jubatum and Phragmites australis.

Our seed germination and seedling growth experiments were similar in set-up and execution, and as expected, results from these experiments were comparable. In these experiments, as in Galinato and van der Valk (1986), germination of the selected species did not decrease gradually with increased salt concentrations. Rather, germination remained fairly constant until the selected species encountered a "threshold" of dissolved salt concentration, beyond which some species were unable to germinate.

The seed bank experiment perhaps best simulates conditions along the north and south shores of Sandhill lakes. The leached treatment roughly approximated water chemistry of groundwater inflow sites along north shores, whereas the recycled corresponded to outflow sites along south shores. We found that the recycled treatment, with its high amounts of dissolved salts, reduced recruitment of Typha spp. seedlings, but had no effect on Scirpus spp. (predominantly Scirpus acutus).

Results from the seed bank study agree with the reported salt tolerances of Typha spp. and Scirpus acutus, with the former being more sensitive to salts (Kantrud et al. 1989). Successful seed germination did not necessarily mean normal good seedling development; in the seedling experiment, the root development of Scirpus maritimus seedlings was impaired at high salt concentrations (14,800 µS/cm). Several species in the seed germination experiment also exhibited abnormal root development at high salt concentrations (14,800 µS/cm); for example, Scirpus maritimus (45.6%) and Scirpus americanus (5.6%) (Appendix L).

There are difficulties in comparing our experimental data directly to our field observations. Nevertheless, the seed bank experiment, using soil samples from Roundup Lake in 1990, gave results that are consistent with the vegetation patterns at the same lake in 1989 (Appendix J). The dominance of Scirpus acutus in the water treatment with high specific conductance and relative lack of Typha spp. in the same treatment imitated dominance of Scirpus acutus along the south shore and Typha angustifolia around the north shore.

Our experiments indicated that Scirpus maritimus, Carex vulpinoidea, Carex scoparia, and Typha spp. could not germinate in water treatments containing relatively high levels of salts suggests that these species also would be unable to germinate under conditions along the south shores of Sandhill lakes. Conversely, species such as Distichlis spicata or Scirpus acutus could occupy these south shores readily (see Appendix J). These latter species, however, had seeds that also could germinate along north shores. Why then are these species not abundant along north shores?

Additional Studies

Our original hypothesis was that vegetation composition in Sandhill lakes differed between north and south shores solely because of differences in water chemistry. Our results suggest that water chemistry may limit the species that can colonize south shores, but other factors must restrict south-shore species to the south shores.

Species that are tolerant of stressful environmental conditions are rarely competitive, according to Grime (1979). Even if salt-tolerant species germinated along the north shores, they might be unable to compete effectively. Although we have not conducted such interspecific competition experiments, other wetland studies have corroborated Grime's prediction. For example, in their study of salt marsh zonation, Bertness and Ellison (1987) found that *Spartina alterniflora* was able to exist in any habitat, but thrived in a more stressful low marsh habitat, which provided a spatial refuge from the competitively superior high-marsh plants. Likewise, Bertness and Ellison (1987) observed that *Distichlis spicata* was stress-tolerant but relatively noncompetitive. Ungar et al. (1979) found that salt tolerance and competitive ability also determined the distribution of *Salicornia europaea* in salt marshes of Ohio.

Species that colonize south shores can do so because their seeds can germinate and seedlings survive in high concentrations of dissolved salts. Species that grow along north shores, we hypothesize, are competitively superior to those of the south shores, and thus prevent south shore species from surviving along north shores. Although other studies have indicated that stress-tolerant species are poor competitors, there is a need to study interspecific competition among wetland species from Sandhill lakes to confirm this hypothesis. Such a study should compare the relative competitive abilities of selected wetland species when exposed to different water chemistries representative of north and south shores of Sandhill lakes.

CONCLUSIONS

Our field studies indicated that both water chemistry and species distributions differed between north and south shores of Sandhill lakes. However, there was no relationship between species distributions and lake elevations. Only the abundance of one species, Distichlis spicata, was correlated with water chemistry (i.e., pH and specific conductance).

Experiments indicated that transplants of adult plants were fairly insensitive to changes in water chemistry; thus, the north-south patterns are not a result of differential adult mortality. Although germination of some selected wetland species was unaffected by increasing concentrations of dissolved salts, other species were unable to germinate at high salt concentrations. Furthermore, some selected species in the seed germination and seedling growth experiments encountered a "threshold" of dissolved salt concentration, beyond which they were unable to germinate and develop. In our seed bank study, the recycled water treatment (i.e., with high amounts of dissolved salts) reduced seed germination and growth of Typha spp., but had no effect on Scirpus acutus. Our experimental data suggest that intolerance of dissolved salts limits the number of species that can colonize south shores. We propose that interspecific competition prevents species normally found along south shores from surviving along north shores.

In summary, vegetation composition along the south shores reflects the abilities of certain species to germinate in the presence of high amounts of dissolved salts. Vegetation composition along the north shores, however, is not the result of failure by salt-tolerant species to colonize these sites. Rather, vegetation composition of the north shores apparently arises when intolerant species outcompete the salt-tolerant ones. If allowed to establish, though, salt-tolerant species can survive along the north shores.

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Table 1. A comparison of 16 Sandhill lakes surveyed in 1988 that had dominant plant species with skewed distributions and McCarraher (1977) data for alkalinity and total dissolved solids; dominant species are those that comprised more than 40% of total vegetation cover

Lake	Elevation (m)	Species Skewed (%)[a]	Alkalinity (mg/l)[b]	Total Dissolved Solids (mg/l)[b]
Miller	1183	53.3	--[c]	--
Maverick	1177	83.8	--	--
Wolf	1170	63.6	--	--
Hessey	1169	46.7	--	--
Brewer	1166	54.5	--	--
Goose	1165	77.8	2080	2580
Shafer	1162	36.4	165	260
Gimlet	1160	41.7	180	285
Roundup	1159	58.3	730	960
Deer	1159	41.7	175	200
Christ	1157	30.0	225	365
Island	1155	28.6	178	280
Crane	1154	25.0	196	365
Hackberry	1154	54.5	--	--
Blue	1153	63.6	200	300
Crescent	1152	86.7	342	470

[a] A species was considered to favor either north or south shores if its cumulative cover for one shore comprised more than 75% of the total vegetation cover, hence a skewed species distribution; cumulative cover is a sum of percent cover measured in 50 quadrats per shore per lake.

[b] When several measurements were made by McCarraher (1977), we listed one taken between May and August .

[c] Data not included in McCarraher (1977).

Table 2. Cumulative cover of *Distichlis spicata* on north and south shores of 16 Sandhill lakes surveyed in 1988

		Cumulative Cover[a]	
Lake	Elevation (m)	North	South
Miller	1183	0	90
Maverick	1177	0	45
Wolf	1170	85	47
Hessey	1169	11	227
Brewer	1166	0	137
Goose	1165	0	5
Shafer	1162	0	67
Gimlet	1160	0	4
Roundup	1159	0	125
Deer	1159	0	0
Christ	1157	0	60
Island	1155	0	65
Crane	1154	0	48
Hackberry	1154	1	65
Blue	1153	0	173
Crescent	1152	15	69

[a] Cumulative cover is a sum of percent cover measured in 50 quadrats per shore per lake.

Table 3. Number by shore of 20 reciprocal transplants at Roundup Lake alive as of 23 May 1990; the chi-square goodness-of-fit analyses used significance levels of 0.10 for 3 df and 0.25 for 1 df; significant values are denoted by *

		Shore				
Species	Source[a]	North	South	X^2	df	$P > X^2$
<u>Scirpus</u> <u>fluviatilis</u>	north	10	6	1.6	1	0.250
<u>Spartina</u> <u>pectinata</u>	north	10	9	0.1	1	0.750*
	north mean	10.0	7.5	1.7	3	0.750
	X^2	0.0	1.7			
	df	1	1			
	$P > X^2$	0.900*	0.250			
<u>Scirpus</u> <u>americanus</u>	south	9	8	0.5	1	0.500
<u>Distichlis</u> <u>spicata</u>	south	10	8	0.4	1	0.500
	south mean	9.5	8.0	0.9	3	0.750
	X^2	0.1	0.8			
	df	1	1			
	$P > X^2$	0.750*	0.250			
	TOTAL	9.75	7.75			
	X^2	0.1	2.5			
	df	3	3			
	$P > X^2$	0.990*	0.500			

[a] Source shore of Roundup Lake, from where the transplants were obtained.

Table 4. Analysis of variance procedures for seed germination experiment with 10 water chemistry treatments (deionized water and nine water samples collected from Crescent Lake National Wildlife Refuge in 1990); significant values (i.e., less than 0.0010) are denoted by *

Species	$F_{1,9}$	Prob > F
Scirpus maritimus	82.50	0.0001*
Carex vulpinoidea	60.80	0.0001*
Carex scoparia	38.75	0.0003*
Distichlis spicata	14.71	0.0050
Scirpus americanus	9.83	0.0139
Carex praegracilis	5.20	0.0520

Table 5. Mean seedling mass of *Scirpus maritimus* and *Carex scoparia* grown hydroponically in 10 water treatments (water samples collected from Crescent Lake National Wildlife Refuge in 1990)

Water Sample	Specific Conductance (μS/cm)	*Scirpus maritimus* (mg)	*Carex scoparia* (mg)
Roundup Depression	14,800	0	0
Goose South	7,000	6	0
Roundup South	1,533	35	3
Hackberry South	1,169	33	3
Roundup North	876	32	4
Goose Northwest	868	27	5
Island Northeast	757	25	4
Hackberry North	654	32	5
Island South	571	25	3
Artesian Well	112	32	7

Table 5. Mean seedling mass of _Scirpus maritimus_ and _Carex scoparia_ grown hydroponically in 10 water treatments (water samples collected from Crescent Lake National Wildlife Refuge in 1990)

Water Sample	Specific Conductance (µS/cm)	_Scirpus maritimus_ (mg)	_Carex scoparia_ (mg)
Roundup Depression	14,800	0	0
Goose South	7,000	6	0
Roundup South	1,533	35	3
Hackberry South	1,169	33	3
Roundup North	876	32	4
Goose Northwest	868	27	5
Island Northeast	757	25	4
Hackberry North	654	32	5
Island South	571	25	3
Artesian Well	112	32	7

Table 6. Analysis of variance procedures for variables in the seed bank experiment using two water chemistry treatments (leached and recycled water); significant values (i.e., less than 0.0050) are denoted by *

	Treatment Mean			
Variable	Leached	Recycled	$F_{8,15}$	Prob > F
Specific conductance (mS/cm)	2.22	7.49	234.86	0.0001*
Scirpus _acutus_ seedlings	7.21	7.14	0.03	0.8630
Typha spp. seedlings	1.38	0.21	16.32	0.0049*
Grass seedlings	0.23	0.38	0.86	0.3838
Forb seedlings	0.38	0.08	4.62	0.0688

Table 7. Observed tolerances to dissolved salts by wetland plant species (from Kantrud et al. 1989)

	Specific Conductance (mS/cm)[a]		
Species	Mean	Minimum	Maximum
Distichlis spicata	17.0	0.5	76.4
Scirpus maritimus	10.3	0.2	76.4
Scirpus acutus	4.3	0.2	37.0
Phragmites australis	3.5	0.1	32.6
Typha angustifolia	3.4	0.4	13.6
Juncus balticus	3.3	0.1	20.1
Spartina pectinata	3.0	tr.[b]	33.5
Lycopus asper	1.9	0.1	32.6
Scirpus fluviatilis	1.9	0.3	6.7
Carex vulpinoidea	1.0	0.1	1.7
Polygonum amphibium	0.6	0.1	2.2
Carex praegracilis	0.3	0.1	3.0
Agrostis stolonifera	0.2	--[c]	--
Scirpus americanus	--	--	--
Carex scoparia	--	--	--

[a] Specific conductance measurements of surface water; these values may differ greatly from measurements of soil extracts (Kantrud et al. 1989).

[b] Trace indicates a measurement less than 0.05 mS/cm.

[c] Measurement was not included in Kantrud et al. (1989).

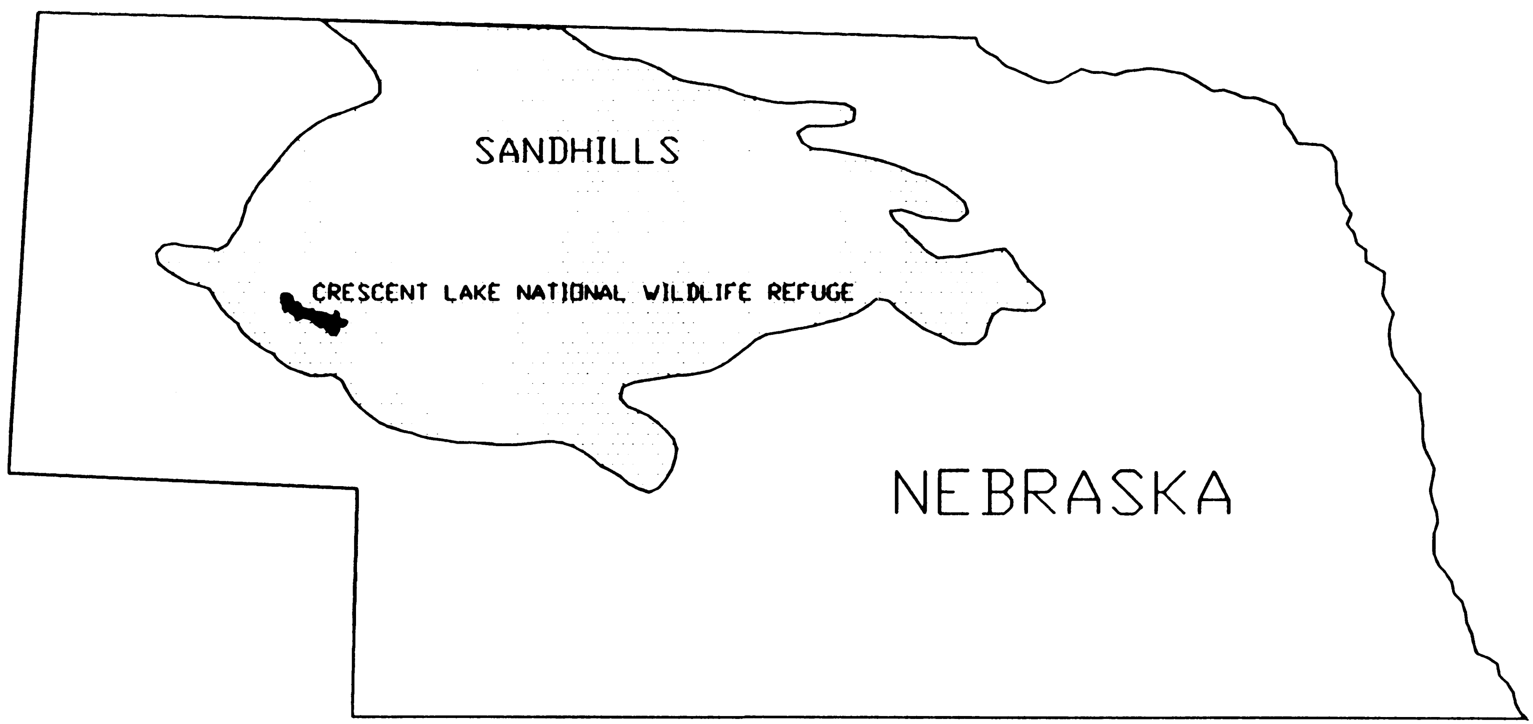

Figure 1. Location of the Sandhills of Nebraska and Crescent Lake National Wildlife Refuge within the Sandhills

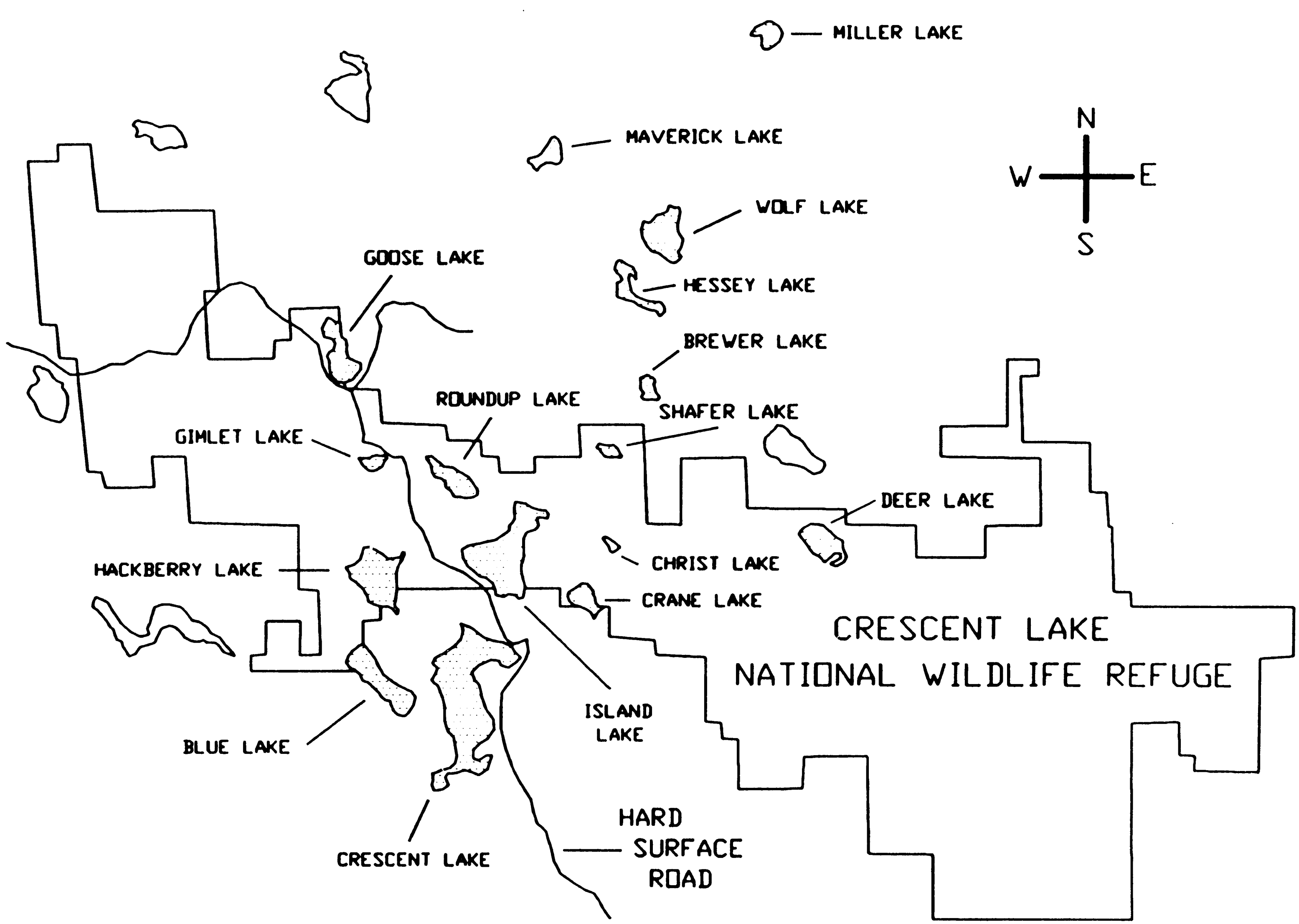

Figure 2. Location of 16 lakes in and adjacent to Crescent Lake National Wildlife Refuge that were sampled in 1988

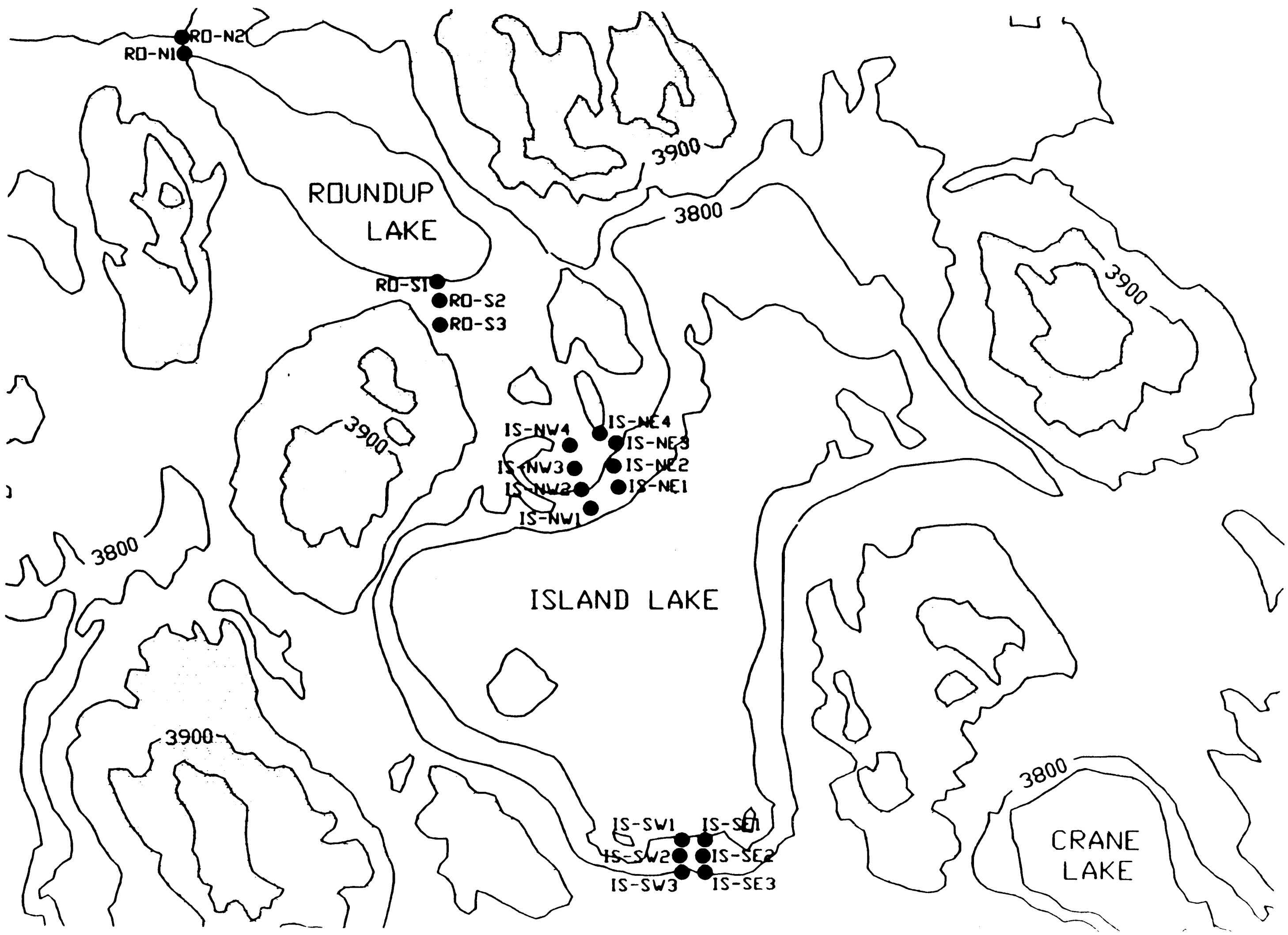

Figure 3. Location of groundwater well lines around Roundup and Island lakes, Crescent Lake National Wildlife Refuge

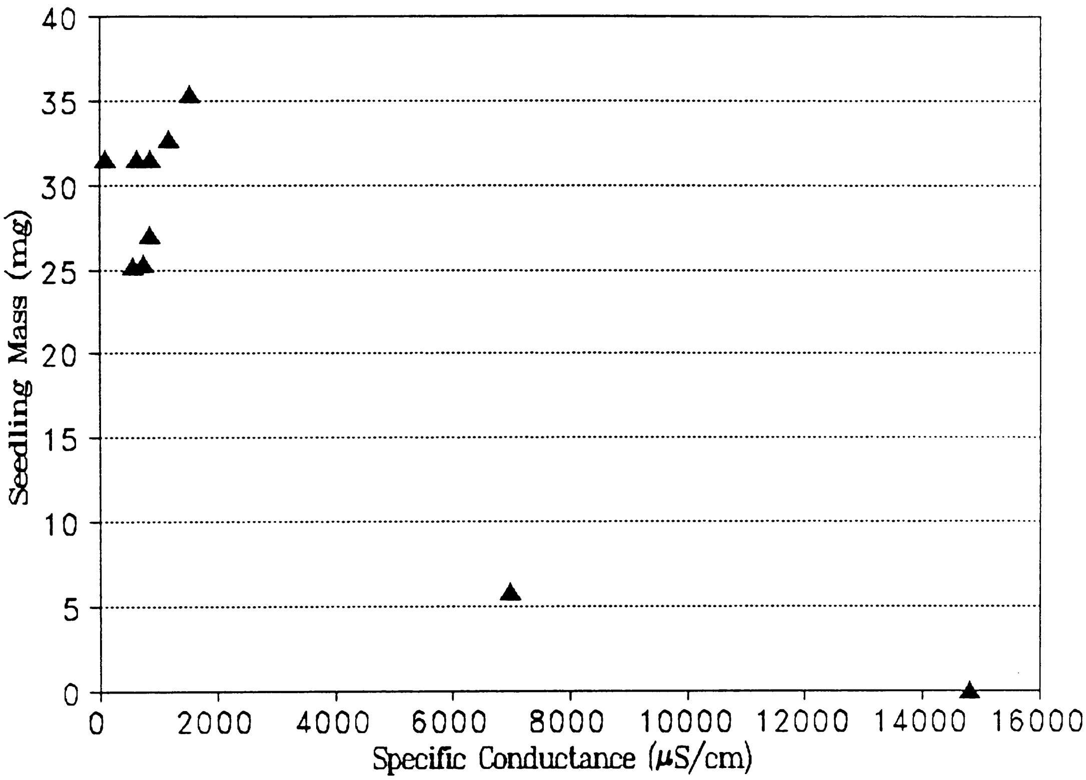

Figure 4. Mass of Scirpus maritimus seedlings versus specific conductance values of 10 water chemistry treatments

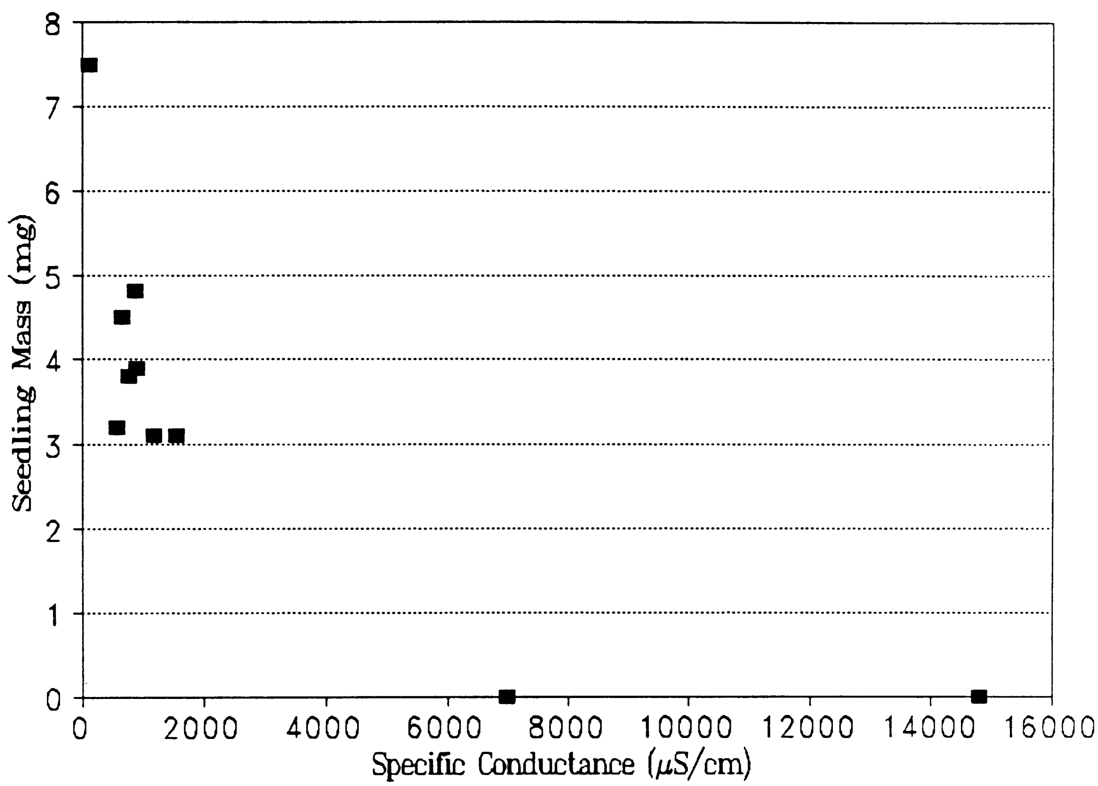

Figure 5. Mass of <u>Carex</u> <u>scoparia</u> seedlings versus specific conductance values of 10 water chemistry treatments

APPENDIX A

Sources of seeds for germination experiment 1990

Species	Site	Date Collected
Carex vulpinoidea	Goose Southwest	21 July 1989
Carex scoparia	Roundup North	24 July 1989
Carex praegracilis	Hackberry South	27 July 1989
Distichlis spicata	Roundup Depression	03 August 1989
Scirpus americanus	Gimlet East	04 August 1989
Scirpus maritimus	Perrin Northeast	04 August 1989

APPENDIX B

Apperture size to control air flow for separating chaff from seeds of selected species for germination study 1990

Species	Apperture (cm)
Distichlis spicata	3.0
Scirpus maritimus	2.5
Scirpus americanus	2.0
Carex praegracilis	1.8
Carex vulpinoidea	1.5
Carex scoparia	1.0

APPENDIX C

Specific conductance measurements of water samples collected from Crescent Lake National Wildlife Refuge between 23 and 24 May 1990

Water Sample	Specific conductance (μS/cm)
Island South	571
Island Northeast	757
Hackberry South	1,169
Hackberry North	654
Roundup South	1,533
Roundup North	876
Goose South	7,000
Goose Northwest	868
Roundup Artesian Well	112
Roundup Depression	14,800
Deionized Water from Iowa State University	25

APPENDIX D

Depth to groundwater table; measurements (cm) taken weekly in 1989 from 19 groundwater wells at Crescent Lake National Wildlife Refuge

		Weekly Depth to Water Table (cm)							
Well	USGS	19 Jun	26 Jun	02 Jul	18 Jul	24 Jul	31 Jul	07 Aug	13 Aug
RO-N1	50	15.2	5.1	22.9	63.5	83.8	86.4	91.4	88.9
RO-N2	49	22.9	35.6	35.6	68.6	81.3	83.8	91.4	81.3
RO-S1	48	12.7	10.2	12.7	27.9	33.0	33.0	43.2	43.2
RO-S2	47	66.0	66.0	68.6	78.7	78.7	81.3	86.4	86.4
RO-S3	21	185.4	188.0	193.0	195.6	195.6	198.1	198.1	200.7
IS-NW1	53	2.5	2.5	10.2	20.3	30.5	25.4	30.5	22.9
IS-NW2	54	22.9	17.8	53.3	43.2	53.3	43.2	50.8	43.2
IS-NW3	55	48.3	45.7	58.4	73.7	81.3	81.3	83.8	76.2
IS-NW4	56	114.3	106.7	119.4	129.5	134.6	137.2	137.2	137.2
IS-NE1	57	53.3	38.1	61.0	76.2	91.4	81.3	91.4	83.8
IS-NE2	58	38.1	27.9	58.4	66.0	73.7	71.1	76.2	71.1
IS-NE3	59	58.4	38.1	63.5	71.1	83.8	78.7	83.8	78.7
IS-NE4	60	177.8	152.4	157.5	167.6	175.3	180.3	185.4	190.5
IS-SW1	45	27.9	27.9	43.2	66.0	76.2	88.9	96.5	96.5
IS-SW2	46	61.0	55.9	66.0	86.4	94.0	101.6	106.7	109.2
IS-SW3	52	83.8	86.4	94.0	109.2	114.3	119.4	124.5	127.0
IS-SE1	44	2.5	0.0	10.2	30.5	48.3	63.5	73.7	76.2
IS-SE2	43	55.9	50.8	66.0	86.4	96.5	101.6	109.2	109.2
IS-SE3	51	101.6	104.1	109.2	127.0	132.1	139.7	144.8	149.9

APPENDIX E

Depth to groundwater table; measurements (in) taken weekly in 1989 from 19 groundwater wells at Crescent Lake National Wildlife Refuge

		Weekly Depth to Water Table (in)							
Well	USGS	19 Jun	26 Jun	02 Jul	18 Jul	24 Jul	31 Jul	07 Aug	13 Aug
RO-N1	50	6	2	9	25	33	34	36	35
RO-N2	49	9	14	14	27	32	33	36	32
RO-S1	48	5	4	5	11	13	13	17	17
RO-S2	47	26	26	27	31	31	32	34	34
RO-S3	21	73	74	76	77	77	78	78	79
IS-NW1	53	1	1	4	8	12	10	12	9
IS-NW2	54	9	7	21	17	21	17	20	17
IS-NW3	55	19	18	23	29	32	32	33	30
IS-NW4	56	45	42	47	51	53	54	54	54
IS-NE1	57	21	15	24	30	36	32	36	33
IS-NE2	58	15	11	23	26	29	28	30	28
IS-NE3	59	23	15	25	28	33	31	33	31
IS-NE4	60	70	60	62	66	69	71	73	75
IS-SW1	45	11	11	17	26	30	35	38	38
IS-SW2	46	24	22	26	34	37	40	42	43
IS-SW3	52	33	34	37	43	45	47	49	50
IS-SE1	44	1	0	4	12	19	25	29	30
IS-SE2	43	22	20	26	34	38	40	43	43
IS-SE3	51	40	41	43	50	52	55	57	59

APPENDIX F

Specific conductance ($\mu S/cm$) measurements taken weekly in 1989 from 19 groundwater wells at Crescent Lake National Wildlife Refuge

		Weekly Conductivity ($\mu S/cm$)							
Well	USGS	19 Jun	26 Jun	02 Jul	18 Jul	24 Jul	31 Jul	07 Aug	13 Aug
RO-N1	50	380	360	400	191	146	262	--[a]	--
RO-N2	49	110	110	100	115	118	122	110	116
RO-S1	48	1980	2610	2900	3000	3260	3320	3320	3480
RO-S2	47	7610	7530	7780	5920	5340	4460	3880	3630
RO-S3	21	2780	3170	3380	3440	3640	3590	3500	3580
IS-NW1	53	250	260	281	296	250	273	253	250
IS-NW2	54	340	360	369	401	373	407	410	410
IS-NW3	55	630	690	705	702	686	635	654	673
IS-NW4	56	510	520	605	--	525	506	514	496
IS-NE1	57	530	570	586	583	493	555	554	548
IS-NE2	58	550	610	583	628	548	588	601	584
IS-NE3	59	410	400	413	427	386	402	408	392
IS-NE4	60	140	150	144	--	128	125	116	115
IS-SW1	45	480	490	583	555	610	607	602	576
IS-SW2	46	490	550	592	528	500	493	475	501
IS-SW3	52	460	450	543	513	473	500	472	466
IS-SE1	44	630	730	831	788	709	728	806	734
IS-SE2	43	320	460	494	498	481	483	473	458
IS-SE3	51	580	590	627	533	471	486	433	414

[a] The measurement could not be taken accurately from the available water sample.

APPENDIX G

pH measurements taken weekly in 1989 from 19 groundwater wells at Crescent Lake National Wildlife Refuge

		Weekly pH Measurements							
Well	USGS	19 Jun	26 Jun	02 Jul	18 Jul	24 Jul	31 Jul	07 Aug	13 Aug
RO-N1	50	6.59	4.55	6.57	6.55	6.78	6.47	--[a]	--
RO-N2	49	6.55	6.60	6.65	6.60	6.65	6.63	6.63	6.61
RO-S1	48	7.37	7.14	7.20	7.25	7.24	7.32	7.39	7.43
RO-S2	47	8.38	8.39	8.37	8.45	8.41	8.40	8.42	8.35
RO-S3	21	7.67	6.25	7.69	7.72	7.69	7.66	7.70	7.68
IS-NW1	53	7.33	7.20	7.27	7.11	7.03	6.83	7.13	7.02
IS-NW2	54	7.07	7.06	7.11	7.17	7.15	7.15	7.19	7.15
IS-NW3	55	6.96	7.05	7.07	7.17	7.25	7.12	7.24	7.68
IS-NW4	56	6.38	6.86	7.34	--	6.85	6.73	6.86	6.87
IS-NE1	57	7.11	7.15	7.13	7.15	7.08	7.01	7.08	7.03
IS-NE2	58	7.12	6.99	7.08	7.09	6.95	6.91	7.06	6.97
IS-NE3	59	7.51	7.49	7.60	7.63	7.59	7.58	7.68	7.63
IS-NE4	60	6.92	7.69	6.87	--	6.58	6.54	6.76	6.77
IS-SW1	45	6.93	6.93	7.19	7.02	7.36	7.59	7.93	7.83
IS-SW2	46	7.15	7.07	7.12	7.15	7.12	7.05	7.29	7.23
IS-SW3	52	7.12	7.11	7.56	7.14	7.06	7.07	7.12	7.44
IS-SE1	44	6.90	6.72	6.72	6.82	6.75	6.94	7.47	7.65
IS-SE2	43	5.34	7.02	7.13	7.12	7.12	7.09	7.19	7.07
IS-SE3	51	5.13	6.78	7.02	6.87	6.76	6.89	6.84	6.86

[a] The measurement could not be taken accurately from the available water sample.

APPENDIX H

Percent soil moisture measurements taken weekly in 1989 from 19 groundwater wells at Crescent Lake National Wildlife Refuge

		Percent Soil Moisture[a]						
Well	USGS	19 Jun	02 Jul	18 Jul	24 Jul	31 Jul	07 Aug	13 Aug
RO-N1	50	37.5	37.7	38.8	27.2	31.8	37.5	33.9
RO-N2	49	26.7	27.6	19.8	18.4	21.2	14.6	14.7
RO-S1	48	26.2	28.3	26.1	23.4	22.8	23.7	20.2
RO-S2	47	8.7	8.0	5.5	4.8	4.3	3.3	4.2
RO-S3	21	2.7	3.1	2.2	2.6	2.1	1.6	3.2
IS-NW1	53	47.2	50.8	49.5	52.4	48.7	50.1	56.0
IS-NW2	54	23.4	24.6	21.9	20.1	21.7	17.7	19.9
IS-NW3	55	22.2	21.8	17.5	18.7	14.4	17.1	14.0
IS-NW4	56	2.7	2.9	2.8	2.5	2.1	1.9	2.1
IS-NE1	57	29.7	30.6	28.7	26.6	28.4	27.4	28.2
IS-NE2	58	23.7	21.9	19.1	19.6	18.9	19.2	21.0
IS-NE3	59	22.0	20.5	16.9	15.5	15.9	16.4	16.4
IS-NE4	60	1.5	1.3	1.2	1.4	1.1	0.9	2.1
IS-SW1	45	24.5	22.1	18.6	17.1	14.5	10.7	9.5
IS-SW2	46	17.9	15.3	10.3	7.2	4.6	4.0	5.1
IS-SW3	52	6.5	4.5	2.6	2.8	2.5	1.8	2.4
IS-SE1	44	26.8	27.8	27.1	24.1	18.1	15.7	19.6
IS-SE2	43	12.9	11.3	5.2	4.4	3.5	3.5	5.7
IS-SE3	51	2.5	2.5	1.7	1.2	0.9	1.1	2.4

[a] Mean percentage calculated from moisture content of four quadrats

APPENDIX I

Cumulative cover of plant species in lakes of the Nebraska Sandhills surveyed in 1988, with the percentage of species with skewed distributions in parentheses; species with shore distributions that exceed 75% of the total also are marked with *

Species	Shore[a] North	Shore[a] South	Total[b]
Blue Lake (63.6%)			
*Distichlis spicata	0	**173**	173
Agrostis stolonifera	45	66	111
Calamovilfa longifolia	59	29	88
*Helianthus annuus	**66**	2	68
*Carex spp.	1	**62**	63
*Juncus balticus	0	**63**	63
*Calamagrostis inexpansa	10	**50**	60
Carex lanuginosa	30	30	60
Ambrosia artemisiifolia	31	17	48
*Polygonum amphibium	**46**	0	46
*Scirpus americanus	0	**45**	45
Brewer Lake (54.5%)			
*Agrostis stolonifera	**137**	21	158
*Distichlis spicata	0	**137**	137
Poa pratensis	51	59	110
Carex praegracilis	42	36	78
Panicum virgatum	50	22	72
Calamovilfa longifolia	42	25	67
*Ambrosia artemisiifolia	**54**	4	58
*Bromus tectorum	6	**44**	50
*Sagittaria latifolia	**38**	10	48
Polygonum amphibium	22	25	47
*Lemna minor	**40**	1	41

Species	Shore North	South	Total[a]
Christ Lake (30.0%)			
Poa pratensis	79	69	148
Agrostis stolonifera	77	70	147
*_Calamagrostis inexpansa_	8	**73**	81
Juncus balticus	35	46	81
Ambrosia artemisiifolia	46	27	73
*_Distichlis spicata_	0	**60**	60
Scirpus fluviatilis	30	30	60
Scirpus acutus	17	41	58
*_Carex lanuginosa_	12	**44**	56
Carex praegracilis	19	34	53
Crane Lake (25.0%)			
Juncus balticus	101	138	239
Poa pratensis	108	75	183
*_Calamagrostis inexpansa_	**101**	28	129
Solidago canadensis	75	28	103
Carex praegracilis	32	67	99
Carex lanuginosa	38	47	85
Ambrosia artemisiifolia	33	38	71
Agropyron smithii	37	13	50
*_Agrostis stolonifera_	**45**	5	50
Panicum virgatum	17	32	49
Calamovilfa longifolia	26	22	48
*_Distichlis spicata_	0	**48**	48

Species	Shore North	South	Total[a]
Crescent Lake (86.7%)			
*Utricularia vulgaris	**185**	0	185
Agrostis stolonifera	90	92	182
Ambrosia artemisiifolia	60	62	122
*Poa pratensis	**111**	0	111
*Distichlis spicata	15	**69**	84
*Calamovilfa longifolia	8	**73**	81
*Stipa commata	5	**59**	64
*Carex praegracilis	**58**	5	63
*Muhlenbergia pungens	0	**60**	60
*Bromus tectorum	1	**54**	55
*Panicum capillare	0	**53**	53
*Scirpus americanus	**51**	0	51
*Hordeum jubatum	**48**	0	48
*Panicum virgatum	**45**	0	45
*Glycerrhiza lepidota	**40**	0	40
Deer Lake (41.7%)			
*Agrostis stolonifera	**175**	40	215
Carex spp.	85	38	123
Calamovilfa longifolia	35	65	100
Polygonum amphibium	25	48	73
*Calamagrostis inexpansa	**54**	18	72
Panicum virgatum	30	42	72
*Scirpus acutus	1	**66**	67
Juncus balticus	26	24	50
*Carex praegracilis	**42**	5	47
Agropyron smithii	32	14	46
*Scirpus fluviatilis	**35**	10	45
Solidago canadensis	14	31	45

Species	Shore North	South	Total[a]
Gimlet Lake (41.7%)			
*_Pilea fontana_	**125**	0	125
Juncus balticus	37	82	119
Agropyron repens	62	30	92
*_Polygonum amphibium_	**83**	8	91
Bromus tectorum	62	24	86
Carex spp.	23	62	85
Lemna minor	10	**50**	60
Calamovilfa longifolia	17	40	57
Solidago canadensis	30	25	55
*_Glycerrhiza lepidota_	7	**41**	48
*_Symphoricarpos occidentalis_	0	**47**	47
*_Carex hystericina_	**35**	10	45
Goose Lake (77.8%)			
*_Polygonum amphibium_	**131**	1	132
*_Bromus tectorum_	**90**	30	120
*_Typha angustifolia_	**100**	20	120
Solidago canadensis	50	55	105
*_Ambrosia artemisiifolia_	**72**	20	92
*_Juncus balticus_	10	**82**	92
*_Poa pratensis_	12	**79**	91
*_Toxicodendron radicans_	15	**70**	85
*_Cirsium arvense_	17	**54**	71
*_Carex lanuginosa_	10	**60**	70
Calamagrostis inexpansa	23	40	63
*_Carex comosa_	**61**	0	61
Carex spp.	34	22	56
*_Urtica dioecia_	**51**	4	55
Scirpus acutus	24	30	54
*_Glycerrhiza lepidota_	0	**42**	42
*_Parietaria pensylvanica_	**40**	0	40
*_Panicum virgatum_	**32**	8	40

Species	Shore North	South	Total[a]
Hackberry Lake (54.5%)			
**Carex praegracilis*	18	**129**	147
Poa pratensis	20	**78**	98
Carex lanuginosa	**43**	51	94
Juncus balticus	36	54	90
Calamovilfa longifolia	29	52	81
**Agrostis stolonifera*	**70**	5	75
**Distichlis spicata*	1	**65**	66
**Polygonum amphibium*	7	**51**	58
Agropyron repens	**51**	2	53
**Bromus tectorum*	0	**47**	47
**Cirsium arvense*	**43**	0	43
Hessey Lake (46.7%)			
**Distichlis spicata*	11	**227**	238
Carex lanuginosa	102	100	202
**Agrostis stolonifera*	**121**	37	158
Carex praegracilis	37	97	134
**Carex* spp.	60	10	70
Panicum virgatum	47	17	64
Scirpus acutus	31	28	59
Ambrosia artemisiifolia	41	15	56
**Glycerrhiza lepidota*	**56**	0	56
Lycopus asper	29	22	51
**Calamovilfa longifolia*	**40**	10	50
**Salsola kali*	**50**	0	50
Erigeron strigosus	32	13	45
Helianthus annuus	15	26	41
**Eleocharis acicularis*	**40**	0	40

Species	Shore North	Shore South	Total[a]
	Island Lake (28.6%)		
Juncus balticus	78	107	185
Carex lanuginosa	62	84	146
Polygonum amphibium	34	76	110
**Agropyron repens*	**86**	15	101
Poa pratensis	60	31	91
Bromus tectorum	32	48	80
**Ambrosia artemisiifolia*	**56**	18	74
Calamagrostis inexpansa	46	25	71
Carex praegracilis	20	50	70
**Distichlis spicata*	0	**65**	65
Carex spp.	37	25	62
Calamovilfa longifolia	20	41	61
Eleocharis palustris	27	26	53
**Agrostis stolonifera*	**42**	10	52
	Maverick Lake (83.3%)		
Agrostis stolonifera	144	75	219
Carex spp.	80	56	136
**Calamovilfa longifolia*	27	**97**	124
**Panicum virgatum*	**102**	2	104
**Phleum pratense*	**71**	7	78
**Polygonum amphibium*	**61**	8	69
**Bromus tectorum*	**42**	13	55
**Salsola kali*	**51**	0	51
**Agropyron repens*	10	**39**	49
**Carex comosa*	0	**45**	45
**Distichlis spicata*	0	**45**	45
**Scirpus americanus*	8	**37**	45

Species	Shore North	South	Total[a]
	Miller Lake (53.3%)		
Bouteloua gracilis	112	145	257
Agrostis stolonifera	84	165	249
Panicum virgatum	67	110	177
*Salsola kali	**105**	0	105
Carex spp.	61	35	96
*Calamovilfa longifolia	**72**	23	95
*Distichlis spicata	0	**90**	90
*Carex lanuginosa	19	**70**	89
Polygonum amphibium	29	32	61
Bromus tectorum	30	29	59
Scirpus acutus	19	35	54
*Stipa commata	11	**35**	46
*Sporobolus cryptandrus	**42**	0	42
*Typha angustifolia	**42**	0	42
*Eleocharis acicularis	10	**30**	40
	Roundup Lake (58.3%)		
*Carex praegracilis	41	**147**	188
Juncus balticus	73	76	149
Poa pratensis	72	76	148
*Bromus tectorum	35	**104**	139
*Distichlis spicata	0	**125**	125
*Solidago canadensis	**112**	3	115
*Scirpus americanus	17	**60**	77
Carex lanuginosa	29	37	66
*Eleocharis palustris	**42**	7	49
Panicum virgatum	23	21	44
Agropyron smithii	33	10	43
*Calamagrostis inexpansa	**43**	0	43

Species	Shore North	Shore South	Total[a]
Shafer Lake (36.4%)			
<u>Agropyron repens</u>	107	142	249
<u>Panicum virgatum</u>	117	72	189
*<u>Carex praegracilis</u>	29	**118**	147
<u>Calamovilfa longifolia</u>	60	35	95
<u>Poa pratensis</u>	27	64	91
<u>Agrostis stolonifera</u>	52	22	74
*<u>Distichlis spicata</u>	0	**67**	67
*<u>Polygonum amphibium</u>	**49**	11	60
*<u>Melilotus alba</u>	52	1	53
<u>Spartina pectinata</u>	23	25	48
<u>Ambrosia artemisiifolia</u>	26	20	46
Wolf Lake (63.6%)			
*<u>Agrostis stolonifera</u>	**214**	1	215
<u>Distichlis spicata</u>	85	47	132
*<u>Ambrosia artemisiifolia</u>	0	**95**	95
*<u>Solidago canadensis</u>	0	**93**	93
*<u>Scirpus acutus</u>	0	**65**	65
*<u>Hordeum jubatum</u>	**52**	6	58
*<u>Carex lanuginosa</u>	**57**	0	57
*<u>Lycopus asper</u>	**38**	7	45
<u>Scirpus americanus</u>	19	23	42
<u>Helianthus annuus</u>	13	27	40
<u>Poa pratensis</u>	29	11	40

[a] Cumulative cover are summed over 50 quadrats per shore per lake.

[b] Species listed comprised more than 40% of total vegetation cover for a given lake.

APPENDIX J

Cumulative cover of plant species along the north and south shores of Island and Roundup lakes in 1989, with the percentage of species with skewed distributions in parentheses; species with shore distributions that exceed 75% of the total also are marked with *

	Shore[a]		
Species	North	South	Total[b]
Island Lake (25.0%)			
Carex lanuginosa	1428	1667	3095
Panicum virgatum	1569	720	2289
Juncus balticus	422	462	884
**Calamagrostis inexpansa*	**834**	20	854
Roundup Lake (100%)			
**Distichlis spicata*	0	**2070**	2070
**Panicum virgatum*	**970**	3	973
**Typha angustifolia*	**325**	44	369
**Scirpus acutus*	13	**324**	337

[a] Cumulative cover are summed over four quadrats per well site per shore per lake.

[b] Species listed comprise more than 5% of total vegetation cover for a given lake.

APPENDIX K

Percent normal germination of seeds in water samples with different conductivities that were collected from Crescent Lake National Wildlife Refuge in 1990; three replicates of 100 seeds received alternating light (8 hours at 30^{o} C) and dark (16 hours at 20^{o} C) conditions

Location	Specific Conductance ($\mu S/cm$)	*Distichlis spicata*	*Scirpus maritimus*	*Carex vulpinoidea*
Island South	571	10.3	42.7	76.7
Island North	757	12.0	38.7	65.0
Hackberry South	1,169	11.0	46.7	77.7
Hackberry North	654	10.7	45.3	53.7
Roundup South	1,533	10.7	39.7	75.7
Roundup North	876	11.7	42.7	72.0
Goose South	7,000	10.0	29.3	28.0
Goose North	868	13.7	39.0	74.7
Roundup Depression	14,800	6.3	0.0	0.0
Deionized Water	25	10.0	36.7	84.7

Location	Specific Conductance ($\mu S/cm$)	*Scirpus americanus*	*Carex scoparia*	*Carex praegracilis*
Island South	571	19.6	65.3	0.3
Island North	757	19.0	64.0	1.3
Hackberry South	1,169	20.0	65.7	1.3
Hackberry North	654	18.0	58.7	0.7
Roundup South	1,533	16.7	64.3	1.7
Roundup North	876	10.0	67.7	1.7
Goose South	7,000	14.6	0.0	0.7
Goose North	868	17.0	62.0	1.3
Roundup Depression	14,800	6.7	0.0	0.0
Deionized Water	25	16.3	73.7	1.0

APPENDIX L

Percent abnormal germination of seeds in water samples with different conductivities that were collected from Crescent Lake National Wildlife Refuge in 1990; three replicates of 100 seeds received alternating light (8 hours at 30^{o} C) and dark (16 hours at 20^{o} C) conditions

Location	Specific Conductance (μS/cm)	*Distichlis spicata*	*Scirpus maritimus*	*Carex vulpinoidea*
Island South	571	2.0	5.7	0.0
Island North	757	1.7	10.3	0.3
Hackberry South	1,169	1.3	6.7	0.0
Hackberry North	654	1.7	6.7	0.0
Roundup South	1,533	1.0	9.3	0.0
Roundup North	876	3.7	6.0	0.3
Goose South	7,000	1.7	20.0	0.0
Goose North	868	2.0	7.3	1.0
Roundup Depression	14,800	0.3	45.7	0.0
Deionized Water	25	2.3	7.0	0.0

Location	Specific Conductance ($\mu S/cm$)	*Scirpus americanus*	*Carex scoparia*	*Carex praegracilis*
Island South	571	0.3	0.0	0.0
Island North	757	0.0	0.0	0.0
Hackberry South	1,169	0.0	0.0	0.0
Hackberry North	654	0.7	0.0	0.0
Roundup South	1,533	0.0	0.0	0.0
Roundup North	876	0.0	0.0	0.0
Goose South	7,000	0.3	33.0	0.0
Goose North	868	0.3	0.0	0.0
Roundup Depression	14,800	5.7	0.0	0.0
Deionized Water	25	0.0	0.0	0.0

APPENDIX M

Analysis of variance procedures for seed germination experiment with eight water chemistry treatments (deionized water and seven water samples collected from Crescent Lake National Wildlife Refuge in 1990; water samples from Goose south and the Roundup depressional wetland were eliminated from the analysis); no significant values (i.e., less than 0.0010) were observed

Species	$F_{1,6}$	Prob > F
Carex praegracilis	3.2567	0.1212
Carex scoparia	1.5543	0.2590
Scirpus maritimus	0.8641	0.3885
Distichlis spicata	0.4206	0.5406
Carex vulpinoidea	0.0638	0.8090
Scirpus americanus	0.0001	0.9918

GENERAL SUMMARY

Vegetation and Soils

The vegetation-soil study was conducted to test if vegetation and soil data were compatible, and hence whether the unified federal method could be used to accurately delineate boundaries of Sandhill wetlands. Furthermore, hydrologic measurements were examined for their usefulness in delineating wetlands.

Vegetation and soil data generally corresponded well with each other, based on General Linear Models procedures for analysis of variance and Duncan's multiple range tests. Prevalence indices calculated for 1988 and 1989 data consistently indicated that the hydric soils supported wetland vegetation. Results were not as consistent for upland soils; two exceptions were the Els, an Entisol, and the Dailey soil series. The upland Dailey series in 1988 supported primarily wetland vegetation, as did the upland Els series at some lakes in 1988 and 1989.

Most likely, the prevalence index for the Dailey soil was atypical for an upland soil because the series was located at a dredged lake. Prevalence indices often are inconclusive when generated by soil series at disturbed sites. Invading ruderal plants associated with disturbance make upland communities appear wetter and wetland communities appear drier when calculating prevalence indices.

Because the Els series supported wetland vegetation somewhat consistently, the possibility exists that the series may be wrongly classified as an upland soil. Many hydric Entisols are difficult to identify because they lack characteristic field indicators (e.g., sufficient clays and organics needed to develop hydric soil colors, mottling, saturation). The Els series exhibits color and mottling that fall within acceptable levels for hydric Entisols. However, the series also could be a transitional soil that contains both wetland and upland components. Because the concept of a soil "series" is artificial, it may allow similar but not identical soil pedons to be combined. Thus, it is plausible that the Els series inadvertently is composed of both hydric and upland pedons.

Finally, a direct measurement of hydrology (i.e., depth to water table) corresponded well to vegetation and soil data. However, an indirect estimate of hydrology (i.e., soil moisture content) was a less reliable indicator of wetland conditions. Although an indirect estimate of hydrology would be appropriate when delineating sites where vegetation and soil data were comparable, a direct measurement of hydrology would be preferable if data were conflicting. With these constraints in mind, the unified federal method overall can be used to accurately designate boundaries of wetlands in the Nebraska Sandhills.

Vegetation and Groundwater

This study examined whether wetland plant distributions corresponded to differences in groundwater chemistry between north and south shores of lakes in the Nebraska Sandhills. One-hundred fifty-nine and 59 species were identified in 1988 and 1989, respectively. All 16 lakes sampled in 1988 had species with skewed distributions (i.e., favoring either north or south shores of lakes). The distribution of _Distichlis spicata_ favored south shores of lakes consistently, whereas _Agrostis stolonifera_ and _Polygonum amphibium_ favored north shores. These preferential distributions corresponded to known tolerances to dissolved salts for these species. Although vegetation patterns differed between north and south lake shores, no trends observed were related to elevations of the 16 lakes.

Environmental parameters measured at groundwater wells in 1989 showed that depth to water table generally decreased as the field season progressed. Similarly, soil moisture content at all well sites decreased over the duration of the field season. No seasonal fluctuations were observed in pH or specific conductance. Correlation analyses performed on 17 dominant plant species and these parameters indicated that only _Distichlis spicata_ was significantly related to pH and specific conductance.

The chi-squared goodness-of-fit analysis of the reciprocal transplant experiment indicated that species from the north shore (i.e., Scirpus fluviatilis and Spartina pectinata) that were transplanted to the south had decreased survival, but some individuals survived nevertheless. Transplanting species from the south shore (i.e., Scirpus americanus and Distichlis spicata) to the north shore had no effect on survival. Apparently, adult plants are relatively unaffected by north and south differences in water chemistry; hence, the north-south vegetation distributions do not result from differential adult mortality. Furthermore, salt-tolerant species were not restricted from north shores by water chemistry; more likely, these species are not abundant along north shores because they are poor competitors.

The seed germination and seedling growth experiments used 10 similar water chemistry treatments that gave comparable results. Analysis of variance procedures for balanced designs indicated differences in germination of Scirpus maritimus, Carex vulpinoidea, and Carex scoparia resulting from water chemistry differences. No significant effects were detected in Distichlis spicata, Scirpus americanus, or Carex praegracilis, however. In the seedling growth study, the 10 water treatments resulted in significantly different means for Scirpus maritimus and Carex scoparia seedling masses. Water treatments with high specific conductance values (i.e., 7,000

$\mu S/cm$ or greater) significantly affected growth, whereas the treatments with low amounts of dissolved salts had no effect on seedling growth.

The seed bank received two water chemistry treatments (i.e., high and low salt concentrations). The water treatments had no effect on the recruitment of Scirpus acutus, grasses, or forbs, based on analysis of variance procedures for balanced designs. However, the germination of Typha spp. seeds was significantly lower in the water treatment with relatively high amounts of dissolved salts, compared to the treatment with the low concentration.

In conclusion, distribution patterns of vegetation in the Sandhills correspond to differences in groundwater chemistry between north and south shores, but not to lake elevations. The distribution of only one species (i.e., Distichlis spicata) was correlated to water chemistry, however. Adult transplants were not sensitive to changes in water chemistry; thus, north-south vegetation patterns cannot be attributed to adult mortality. Selected species exhibited different tolerances to dissolved salts, with regard to their germination and growth. These experiments suggest that water chemistry influences recruitment, which in turn affects vegetation composition. In a further interpretation, vegetation composition along the south shores of Sandhill lakes reflects the ability of some species to germinate in high levels of dissolved salts. Vegetation composition along north shores is not the ability of salt-tolerant species to colonize these sites, however. Rather, vegetation composition along north shores most likely results when intolerant species outcompete salt-tolerant ones.

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